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## ECOLOGY, EVOLUTION AND SOCIETY<sup>1</sup>

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ECOLOGY deals with the interrelationships between the organism and its environment, both physical and biotic. The concept of the organism, however, is complex and various levels of biological organization occur. Viruses, cells, multicellular organisms, metameric organisms, metamorphic organisms, colonial organisms, species populations, aggregated populations, cyclomorphic populations, sex pairs, family units, social units and certain types of ecological communities, each represent a level of individuality with organismic attributes.<sup>2,3</sup> Each living unit, in other words, has its external environment.

The environment of a cell, if it be a protozoan, may be treated by the ecologist, but the environment of a cell, if it be in a tissue or organ of a multicellular organism, is usually treated by the physiologist. The environment of a red blood cell is thus studied by a physiologist, but the environment of a malarial parasite within the erythrocyte is the province of the parasitologist who comes within the broad field of ecology. The environment of an embryo is studied by the embryologist while the environment of a larva is within the province of the ecologist. The social environment of an individual human is studied by the sociologist, the psychologist, the economist, the

<sup>1</sup> Presidential address delivered before The Ecological Society of America, Dallas, Texas, on December 29, 1941.

<sup>2</sup> A. E. Emerson, *Amer. Midland Nat.*, 21: 182-209, 1939.

<sup>3</sup> F. E. Clements and V. E. Shelford, *Bio-Ecology*. vi+425 pp. New York: John Wiley and Sons, 1939.

anthropologist, the geographer and the historian, while the social environment of the individual ant is again the interest of the ecologist who also treats the external environment of the ant colony. If the environmental factors are correlated, as they often are, with hereditary, physiological, developmental or behavioristic phenomena, they are immediately brought into the reports of the geneticists, physiologists, embryologists and psychologists.

I should not interpret the difficulties involved in setting arbitrary lines of demarcation between ecology and various sciences as indicative of a lack of a central ecological theme. Granting the existence of various levels of integration among organisms and the complexity of the environmental effects, a basic dichotomy is still possible between the living unit and its environment even without precluding greater units that might incorporate both organism and environment.

I should rather interpret the overlap of concepts and interests as indicative of the great benefit that ecologists may derive from an understanding of the principles discovered by other sciences and the great value that ecology can be to other scientific fields.

Ecology has made some of its greatest advances in the study of the integrative patterns of organization in the ecological community and the dynamic effects of environmental factors upon the organism. These may be considered as pertaining to the three dimensions of space. A fourth dimension involving time is the base of reference in the study of ecological succession which may be likened to the ontogenetic sequence of the individual organism. Migration together with diurnation, aspection and annuation are also phases of these space-time dimensions.<sup>4</sup> An extension of the spatial and time dimensions is found in the different ecological origin of various species in the community succession. In the Indiana dunes bordering Lake Michigan, a species of termite (*Reticulitermes tibialis*) is found from the foredunes

<sup>4</sup> *Ibid.*

through the oak stages, but another species (*Reticulitermes flavipes*) is found in the climax beech-maple forest on both sand and clay. The first species, however, is found in the relatively dry post-climax and pro-climax valley woodlands of the states west of the Mississippi and the second species is found in the relatively mesic seral stages in the eastern states. These species also have diurnal and seasonal cycles. An understanding of the time sequence of communities in one area thus involves a knowledge of the spatial origins and various ecological adjustments of the species as well as their immediate community relations.

I propose in the limited time at my disposal, not to mention my limited capacity and perspective, to place emphasis upon a fifth dimension of ecological study, also involving time, namely evolution. We are all aware in our ecological studies that the functional correlation between an organism and a factor in the ecological community is not to be understood wholly by studying the present relationship. Even a succession of communities is not completely explained through an understanding of present day factors operating on existing species. The dynamics of an existing interaction has a chronological background that stretches further than the chronological succession of existing factor patterns. A species of tiger beetle on sand in the early stages of a dunes succession attained its bilaterality before its segmentation, its compound eyes before its tracheae, its legs before its wings, its mandibles before its larval stage and its predatory adjustments before its adjustments to narrow ranges of soil moisture. Not only this, but most of the adaptations to this present environment which help to explain why this species is found where it is and why it is absent from other somewhat similar habitats were developed in part at least in other ecological situations inhabited by the ancestors of the existing species (an aspect of preadaptation). In addition, it retains in its organization and in its development, functionless characteristics which were

functional in its ancestors living under different ecological conditions. It is as impossible for an ecologist to explain certain obvious facts of ecological pattern by recourse only to the existing spatial dimensions and the time dimension of the successional sequence, as it is for an embryologist to explain certain obvious facts of embryological pattern through an investigation limited to the dynamics of the immediate organic spatial pattern in its ontogenetic sequence.

I may sum up this introduction by stating that an understanding of evolution is important to an adequate understanding of an organism, an organism in its environment, or an ecological community. Ecologists may be proud of the fact that they are lineal scientific descendants of the nineteenth century naturalists who contributed to our knowledge of the mechanisms of evolution. Ecology, to use one of Wheeler's similes, is hardly more than a branch from the natural history stolon which is so slightly differentiated that it may be a question whether it is a branch or the stolon itself.

I am reminded of the discussion between W. C. Allee and the ornithologist, Rudyerd Boulton. Allee stated that ecology was scientific natural history that became self-conscious at the turn of the century. A light dawned on Boulton who remarked, "Now I know what an ecologist is; an ecologist is a self-conscious naturalist." I hardly know of a better definition and we may well pride ourselves in our capacity as naturalists along with the taxonomists and geneticists who would also claim close scientific kinship to Lamarck, Darwin, Wallace, Haeckel and Weismann. However, we must carry on the inquiries of these men if we are to point to them with pride. What can modern ecology contribute to an analysis of evolutionary dynamics?

I think we may well leave the causes of hereditary variation to the geneticists. It is true that environmental factors such as chemicals, heat, ultraviolet light and radio-active emanations may induce mutations and



there may even be some ecological distribution of such causative factors. Chance chromosomal and gene mutations may immediately effect the ecological adjustments, sometimes in a beneficial manner (another aspect of preadaptation).<sup>5</sup> However, mutations, especially in their complex patterns, seem to have no ecologically directed functional relation to the environment, leaving selection and isolation aside.

Since the days of Lamarck, many investigators have sought for data on the inheritance of acquired, environmentally induced, somatic characters. Although it is probably too early to become rigidly dogmatic on this point, I do believe it is safe to say that the data in support of any such Lamarckian mechanism are largely lacking and that other mechanisms seem to be far more adequate in explaining the vast majority of known evolutionary phenomena.

The ecologist has much to contribute to two main phases of evolutionary dynamics, however, namely isolation and natural selection. In other words, ecological factors have an important influence on evolutionary divergence and adaptation. Also the initial stages of an evolutionary divergence involve population units. Species, subspecies and races are population concepts and the ecologist is interested in the intraspecific environment of the individuals within such populations and the environmental effects upon population physiology and integration.

All evolutionary divergence involves reproductive isolation in some form. As far as we know, genetic variation within populations is constantly occurring although the rate may differ in different genes, in different chromosomes, in different organisms and in different populations. Not only do qualitative genetic differences occur in isolated populations which can not spread their chromosome patterns to their closest genetic populations without interbreeding, but a quantitative shift in allele

<sup>5</sup> G. L. Stebbins, Jr., *AM. NAT.*, 76: 36-45, 1942.

distribution may distinguish recently isolated populations. If all other factors remained constant except that a different sized population became isolated from the original population, a gradual divergence would occur through accidental fluctuation of the concentration of single genes.<sup>6,7</sup> Large fluctuations in the effective breeding population (population waves) act as partial isolating agents. The elementary evolutionary process is often a change of gene-frequency rather than mutation.<sup>6</sup> Also larger populations are likely to show wider ranges of variability than relatively smaller populations because of the tendency of closely inbreeding populations to develop homozygosity.

There are numerous types of isolating mechanisms which prevent population interbreeding. Lack of sexual reproduction in parthenogenetic and vegetatively reproducing organisms obviously prevents the sharing of genetic systems except through clonal descent.<sup>8</sup> In sexual species, fertility impairment, inviability of the hybrids and adult sterility all contribute to reproductive isolation, but are essentially physiological, genetic or embryological phenomena. Isolation of populations through geological time may produce chronological clines, but these are primarily the problem of the paleontologist. The ecologist, however, may make important contributions to the concepts of geographical, habitat, annual, seasonal, diurnal and sexual isolation.

Geographical isolation (which could be more exactly subdivided into spatial and topographical isolation) is generally accepted as having an important bearing upon evolutionary divergence. In order to analyze the complex factors correlated with geography, however, it is necessary for the ecologist to search for cases where one

<sup>6</sup> S. Wright, "The Statistical Consequences of Mendelian Heredity in Relation to Speciation." pp. 161-183. In J. Huxley, "The New Systematics." Oxford, 1940.

<sup>7</sup> N. W. Timofeeff-Ressovsky, "Mutations and Geographical Variation." pp. 73-136. In J. Huxley, "The New Systematics." Oxford, 1940.

<sup>8</sup> K. B. Raper and C. Thom, *Am. Jour. Bot.*, 28: 69-78, 1941.

or a few factors differ while others remain constant. Such naturally occurring cases sometimes have all the analytic values of controlled experiments. For example, populations of Amazonian ant-thrushes differ on the right and left banks of the Amazon, although there would seem to be no correlated habitat differences.<sup>9</sup> These birds, although capable of flight, seem to be confined to deep woods and avoid crossing such open spaces as wide rivers. The only known correlated factor with such evolutionary divergence, therefore, is the isolation of the populations by means of the river barrier. Closely similar ecological habitats often are inhabited by different closely related species in such situations as the opposite banks of the Grand Canyon, separated mountain ranges, oceanic islands, separate caves within larger cave systems, etc. When such topographical localities differ ecologically, differential selection is probably also operating in addition to isolation, thus complicating the factorial analysis.

Habitat isolation (sometimes called ecological isolation<sup>10</sup>) of species in the same geographical area is a common enough observation. Worthington<sup>11</sup> gives interesting cases of speciation of fishes (*Haplochromis*) in Lake Victoria correlated with different types of food. Fulton<sup>12</sup> experimentally crossed two subspecies of crickets (*Nemobius fasciatus fasciatus* and *N. fasciatus tinnulus*) with song distinctions living in the same geographical region but in different habitats. Successional series often show a sequence of closely related species which are geographically contiguous in at least portions of their ranges. Probably the best examples of habitat isolation, however, are to be found among the monoxenous herbi-

<sup>9</sup> R. Boulton, personal communication.

<sup>10</sup> T. Dobzhansky, "Genetics and the Origin of Species." p. 257. (2d edition.) New York: Columbia Univ. Press, 1941.

<sup>11</sup> E. B. Worthington, "Geographical Differentiation in Fresh Waters with Special Reference to Fish." pp. 287-302. In J. Huxley, "The New Systematics." Oxford, 1940.

<sup>12</sup> B. B. Fulton, *Ann. Ent. Soc. Amer.*, 26: 368-376, 1933.

vores,<sup>13</sup> parasites, and symbiotic guests of social insects.<sup>14, 15</sup> Of course such cases usually involve adaptation. In some instances, however, natural selection may be a minor factor. Certain herbivores may be forced to eat plants which they do not normally eat and adults raised from such experimental stocks will oviposit on the new plant when given a choice (Hopkin's host-selection principle). Thorpe<sup>13</sup> cites an experimental case of host selection by an Ichneumonid (*Nemeritis canescens*) and concludes, "The theoretical importance of such a conditioning effect is that it will tend to split a population into groups attached to particular hosts or particular food-plants, and thus will of itself tend to prevent cross-breeding." Territoriality among breeding birds also is the result of conditioning and the young may return to the locality of their origin for subsequent breeding. Thus an isolating mechanism between populations in local regions may be inaugurated without ecological adaptation. Such territoriality might give rise to species divergence if similar ecological areas are sufficiently isolated. I cite an instance to illustrate the hypothetical action of such factors in the case of the Eastern and Western Wood Pewees (*Myiochames virens* and *M. richardsonii*) which overlap in wintering range in Central and South America but breed in separate areas without known adaptive adjustments. The species are remarkably close in their morphological and color characters, but differ somewhat in their calls.

Annual isolation within the same geographical and habitat areas may possibly have some effect upon the divergence of species with life cycles extending two years or more. The races of the periodical cicada (*Magicicada septendecim*) may be partially isolated in this way and the races of the Pink Salmon (*Oncorhynchus gorbuscha*)

<sup>13</sup> W. H. Thorpe, "Ecology and the Future of Systematics," pp. 341-364. In J. Huxley, "The New Systematics." Oxford, 1940.

<sup>14</sup> A. E. Emerson, *Ann. Ent. Soc. Amer.*, 28: 369-395, 1935.

<sup>15</sup> C. H. Seevers, *Ann. Ent. Soc. Amer.*, 31: 422-441, 1938.

which breed in the same streams in alternate years are differentiated.<sup>16</sup>

Seasonal isolation is difficult to separate from possible selective forces, although statistical correlations may indicate that isolation rather than selection is sometimes the main cause of evolutionary divergence. Dobzhansky<sup>17</sup> has recently brought together several cases of seasonal breeding differentiation in otherwise closely related species occupying the same geographical and ecological habitats in at least part of their ranges. Differences in the flowering season of otherwise closely related species of plants and in the mating period of closely related species of butterflies are discussed. Piersol<sup>18</sup> gives a case of seasonal differentiation of breeding among salamanders (*Ambystoma jeffersonianum* and *A. maculatum*) in the same pond. However, seasonal isolation will be best illustrated by more data from experiments which prove no hybrid sterility or inviability. Hogben<sup>19</sup> refers to the case of two species of moths, one (*Eupithecia innotata*) feeding on *Artemisia* and the other (*E. unedonata*) emerging earlier and feeding on *Arbutus*. Pupae of the *Arbutus* species were cooled delaying their emergence and thus they were mated with the *Artemisia* species and fertile hybrids were produced.

Diurnal isolation may play a role in speciation. Larval microfilariae (*Wüchereria bancrofti*) usually show nocturnal periodicity in the human blood stream and are thus adapted for transmission by the night-biting mosquitoes (*Culex fatigans*, etc.). A non-periodical biological race or species of this parasite, morphologically similar to the periodical form, is transmitted by a day-biting mosquito (*Aedes variegatus*) whose distribution is closely correlated with the non-periodic filaria in certain islands of

<sup>16</sup> F. A. Davidson, personal communication.

<sup>17</sup> T. Dobzhansky, "Genetics and the Origin of Species." (2d edit.) New York: Columbia Univ. Press, 1941.

<sup>18</sup> W. H. Piersol, *Trans. Roy. Canad. Inst.*, 17: 57-74, 1929.

<sup>19</sup> L. Hogben, "Problems of the Origins of Species." pp. 269-286. In J. Huxley, "The New Systematics." Oxford, 1940.

the Pacific (Fiji, Samoa, Tokelau, Wallis, Ellice Islands, Philippines, and Tahiti).<sup>20</sup> This case illustrates the possible isolating effect of daily ecological fluctuations although the influence of selection is not eliminated.

Closely related species of fishes (*Pomoxis nigro-maculatus* and *P. annularis*), with similar food, food-habits and general behavior, occur together in the Illinois and Ohio rivers and a few interspecific hybrids are known. One (*P. nigro-maculatus*) shows a nocturnal activity rhythm and the other (*P. annularis*) is diurnal, thus indicating that these species are reproductively isolated through their different activity cycles. In the same family (Centrarchidae), the forms that hybridize freely have activity periods which are the same or broadly overlap.<sup>21</sup>

Sexual isolation involving both mechanical and psychological mating actions properly are ecological because one sex is a part of the environment of the opposite sex. Anything that interferes with the function of species or sex recognition may be an isolating mechanism. Crampton<sup>22</sup> states that sinistral and dextral snails (*Partula*) might be unable to mate thus mechanically isolating population units. Psychological or behavior isolation is particularly well shown in certain cases. Dice<sup>23</sup> has recently reported an overlap of the ranges of two species of mice (*Peromyscus leucopus* and *P. gossypinus*). In nature, hybrids are rarely found, but in the laboratory the two species interbreed readily and produce viable offspring. The Eastern and Western Meadow Larks (*Sturnella magna magna* and *S. neglecta*) do not seem to hybridize in nature but they do cross in the laboratory and produce offspring.<sup>24</sup> In the prairie habitats west of Chicago these two species may be found nesting in the same field.

<sup>20</sup> P. H. Manson-Bahr, "Manson's Tropical Diseases," pp. 750, 950. (11th edit.) Williams and Wilkins Co., Baltimore, Md., 1940.

<sup>21</sup> O. Park, personal communication; data from C. L. Hubbs, D. H. Thompson, G. W. Bennett, C. L. Turner and W. P. Spencer.

<sup>22</sup> H. E. Crampton, *Carneg. Inst. of Washington, Publ.*, 410: 1-335. p. 188, 1932.

<sup>23</sup> L. R. Dice, *Jour. Mammalogy*, 21: 14-23, 1940.

<sup>24</sup> G. B. Saunders, personal communication.

Where possible, I have used examples of ecologically isolated species showing hybridization in order to analyze the factors with greater accuracy. The analytical value of subspecies and races in this connection is obvious. However, sterility between species is common even though ecological isolation is involved. Wright<sup>25</sup> states, "It appears probable that the more or less complete cross-sterility that permanently separates most good species from their nearest allies is usually a by-product of the gradual accumulation of genetic differences in populations isolated at first merely by geography, habitat, etc."

Darwin emphasized natural selection as the basic mechanism of evolution. To-day we feel that our knowledge of the genetics of variation and the role of isolation gives us a clearer picture of evolutionary dynamics. However, natural selection is still of tremendous importance, not so much as the prime factor in the origin of all species as it is in the explanation of practically all complex adaptation. Adaptive characters which have been analyzed genetically almost always are multiple gene effects and there is every reason for assuming that such complex gene patterns did not arise simultaneously. Adaptation is such a universal phenomenon and selection is such a satisfactory mechanism that it is surprising to find controversy on the general principle still occurring.

Adaptation is characteristic of the higher taxonomic categories, but is not always so easily demonstrated in species and subspecies, and certainly all specific characters do not seem to be functional. The explanation may be that the more adapted species survive and may then speciate further with the concomitant extinction in time of the less adapted species which have speciated through neutral variation and isolation. Also, as more adapted groups arise, they form the focal points for adaptive radiation into niches occupied by less efficient types.

<sup>25</sup> S. Wright. In J. Huxley, "The New Systematics." Oxford. pp. 161-183, 1940.



Noble,<sup>26</sup> however, points out that the degree of adaptive modification to the habitat bears no relation to the degree of specialization attained in phylogeny and gives the case of the adjustments of a primitive frog (*Ascaphus truei*) to mountain streams as an illustration.

Although adaptation is usually the result of a great many factors operating over long periods of time on complex organic systems, the ecologist must needs demonstrate selection as a factor at the initial stages of evolutionary divergence if he is to understand the influence of selective factors relatively uncomplicated by other factors. Correlations between environment and functional characters beyond the probabilities due to chance are the usual data indicating the operation of selective pressures. Such statistical correlations show such characteristic patterns that they may be used in prediction. For example, it is possible on occasion to predict the discovery of a new species of a certain genus in a certain locality and possessing certain specific characteristics. Wallace, having found a number of mimicry pairs of species in two genera of butterflies (*Delias* and *Huphina*) on various islands in the East Indies, but having found only a single species of the mimicking genus (*Huphina*) on Timor, predicted that a new species of the model genus (*Delias*) would be found on that island having certain color characteristics. Thirty-four years later his prediction was realized.<sup>27</sup>

Survival statistics and toleration experiments may be resorted to for better correlations demonstrating the possible action of selective factors. Among some interesting examples of such an experimental approach are those of Carrick<sup>28</sup> on color adaptations of insects in Britain, Isely<sup>29</sup> on protective coloration of grasshoppers in Texas, Talbot<sup>30</sup> on humidity toleration of ants in the

<sup>26</sup> G. K. Noble. "The Biology of the Amphibia." New York: McGraw-Hill Book Co., xiii + 577 pp. p. 87. 1931.

<sup>27</sup> F. A. Dixey, *Trans. Ent. Soc. London*, 1920: 208-211, 1920.

<sup>28</sup> R. Carrick, *Trans. Roy. Ent. Soc. London*, 85: 131-140, 1936.

<sup>29</sup> F. B. Isely, *Ecology*, 19: 370-389, 1938.

<sup>30</sup> Mary Talbot, *Ecology*, 15: 416-439, 1934.

Chicago region, and Hiesey, Clausen, and Keck<sup>31</sup> on climatic survival of different ecotypes among plants.

Occasionally experiments with excellent control over many factors have been performed in nature or unwittingly through human agencies. Such a case is to be found in the distribution and survival of the house rats. The Black Rat originated in the tropical orient and spread into northern Europe in medieval times. In the eighteenth century it was largely displaced by the Norway Rat which originated on the temperate steppes of Asia. Distributed by commerce, these two allied species have been and are being introduced to all parts of the world, but the Black Rat has established itself in the tropics while the Norway Rat has survived in temperate regions such as northern United States and Argentina. In competition, these species demonstrate their adaptation to the climatic conditions of their original areas. Without competition, the tropical Black Rat could and did overrun the human habitations as far north as Upsala, Sweden, where it was described by Linnaeus.

The ecologist studying adaptive similarities becomes aware very soon of functional similarities showing correlations with the environment but not with the taxonomic and phylogenetic patterns. Convergent evolution quite clearly shows how environmental selective pressures may move different organismic systems toward striking analogous functional resemblances. Cases may be cited all the way from class characters such as the wings of insects and birds or the eyes of vertebrates and squids to the species and race characters of black rodents of different genera on the black lava flows of New Mexico<sup>32</sup> and the remarkable locomotion of the Sidewinder (*Crotalus cerastes*)<sup>33</sup> and the African viper (*Cerastes vipera*) on the loose sands of the California and Sahara deserts.<sup>34</sup>

The positive action of selection of genetic variations

<sup>31</sup> W. M. Hiesey, J. Clausen, and D. D. Keck, *AM. NAT.*, 76: 5-22, 1942.

<sup>32</sup> S. B. Benson, *Univ. Calif. Publ. Zool.*, 40: 1-70, 1933.

<sup>33</sup> W. Mosauer, *Ecology*, 16: 13-27, 1935.

<sup>34</sup> W. Mosauer, *AM. NAT.*, 64: 179-183, 1930.

seems to be by far the best explanation of the origin of both endo- and exo-adaptations, but certain cases involving degenerative evolution have been more difficult to explain. Such degenerative organs as vestigial eyes are characteristic of cave species showing the same type of habitat correlation as adaptive characters, and yet such vestiges in themselves are hardly adaptive. However, modern genetics is able to supply a satisfactory explanation of such evolutionary trends. Several experimentally demonstrated principles may be assumed. (1) Each gene or genetic factor effects many characters. (2) Each character is effected by many genes. (3) Mutation of any single gene may occur at a statistically predictable rate (mutation pressure). (4) The effect of a mutation on a functional character is almost always deleterious or degenerative. (5) Selection acts upon the whole organismic unit and not alone upon the parts or definitive characters. (6) Elimination or weakening of a selective pressure will in time result in the degeneration of the functional character through the action of mutation pressure. It thus follows that if selection favors an increased development of one character and another character has a diminished survival value in a given ecological situation, there will be a shift in the alleles in many series with a consequent degeneration of the character losing importance.<sup>35</sup> Through the action of these tendencies, we have a reasonable explanation of non-functional vestigial structures and recapitulative phenomena.<sup>36</sup> We may thus understand why the eyes of many unrelated species confined to the cave environment undergo convergent degeneration in correlation with the functional enhancement of tactile organs or other useful characters, and at the same time understand why vestigial eyes are quite commonly present in these blind species. The complex genetic system correlated with an ancient and important adaptive character which has lost

<sup>35</sup> S. Wright, in A. E. Emerson, *Ecol. Monogr.*, 8: 247-284, 1938.

<sup>36</sup> H. V. Wilson, *AM. NAT.*, 75: 20-30, 1941.

survival value in its present environment could not be eliminated suddenly without effecting many other vital characters. The universality of evolutionary degeneration of some ancient exo- and endo-adaptations in every organism may then be explained without recourse to Lamarckian mechanisms unsubstantiated by experimental data.

Intraspecific adjustments which adapt individuals of different generations to different environments (cyclo-morphic populations) or adapt the individual to other individuals within the population are results of complex evolutionary processes. Aggregated populations of organisms have recently been experimentally investigated by leading ecologists, particularly by W. C. Allee, T. Park, and their associates. As a student of social insects, I am particularly interested in this phase of ecology and find it of considerable importance in the clarification of certain evolutionary principles. Not only is an analysis of integrative factors of populations from simple aggregations to complex societies of importance to the ecologist who is constantly confronted with these phenomena in the field, but the evolution of cooperative systems leads us to a better understanding of evolutionary mechanisms, ecological communities and human societies.

That various levels of aggregated populations show adaptation has been demonstrated by Allee<sup>37,38</sup> through differential survival values of different numbers in toleration experiments on simply aggregated groups, and my own studies of the adaptive characteristics of termite nests built by highly social populations.<sup>39</sup> Some of the most remarkable social adaptations are found among the slave-making species of ants. Convergence is also amply demonstrated in social groups. Even among the insects,

<sup>37</sup> W. C. Allee, "Animal Aggregations." Univ. Chicago Press. 431 pp., 1931.

<sup>38</sup> W. C. Allee, "The Social Life of Animals." W. W. Norton and Co., New York. 293 pp., 1938.

<sup>39</sup> A. E. Emerson, *Ecol. Monogr.*, 8: 247-284, 1938.

highly complex societies arose convergently several times, the most striking example being the similar organization of ants and termites, while the complex societies of insects and men are predominantly convergent and analogous. Some of the convergent analogues in the societies of insects and men are social integration through signals, chemical agents, and activity gradients; social symmetry and relatively stable patterns of organization; social dominance; replication of patterns (polyisomerism); functional specialization and division of labor of diverse societal units through classes or castes (anisomerism); ontogeny of social organization; phylogeny of the social system; social divergence and convergence; recapitulation during ontogeny; degenerative evolution and vestigial social characters; social variation and selection of social and familial units; and the dynamic maintenance of population equilibrium of integrated social units (logistic curve of population growth). These analogues not only show a remarkable similarity between insect and human social systems, but in many instances they are also attributes of sub-social populations and individual organisms. Particularly in the case of the insects, the convergence between the organismic coordination and the social coordination is so complete that one may speak of the society as a supraorganism guided in its evolution by many factors that have also guided the evolution of the individual organism.<sup>40</sup> Thus we may find social examples of homology, instinct, hormones, physiological gradients, various types of symmetry, mechanical reactivity, ecological orientation, sterile somatic differentiation, reproductive adaptations, periodicities, size control, defensive adaptations, physiological isolation, budding, and duplications, and all these analogues have highly similar correlated factors chronologically preceding the appearance of these characteristics. However, as can be well illustrated by the genetic determination of sex in the higher social animals, homolo-

<sup>40</sup> A. E. Emerson, *Amer. Midland Nat.*, 21: 182-209, 1939.

gies are between the solitary organism and the individual within the society showing that the social supraorganism is an aggregation of individual organisms and not an extension of the organismic homologies of the individual.<sup>40</sup>

In spite of many common analogous attributes, human society shows fundamental differences from insect social systems and these must also be analyzed. Social insects are not separated from solitary insects by a striking quantitative differential in learning capacity. Also leadership as a result of conditioning is not as apparent as among men and the higher vertebrates. Correlated with these generalizations, human social evolution has taken place with great rapidity compared to the slow evolution of insect societies. We also find such human social systems as political government, law, police, educational institutions and religion lacking among the insects.

The basic reason for such differences may be explained by the addition of a new type of hereditary mechanism. Besides the usual biological heredity through genic patterns in the chromosomes which determine relatively stereotyped development by means of enzyme chains, the human species has developed a new mechanism which we call social heredity or culture.<sup>41</sup> This outstanding human attribute forms the valid division line between social and biological sciences. Man has symbolized his experiences and values by means of money, tools, pictures, and language, and these are transmitted through exchange, gestures, talk, writing, drawing, photography, printing, telegraph, telephone and radio, not only to his immediate associates, but to all parts of the world and to all succeeding generations. Thus our social patterns are repeated without involving the germ plasm and, in order to evolve socially, we do not need to wait for the genes to undergo favorable mutation and for the slow process of natural selection to sort out beneficial gene effects. Correlated with this additional mechanism of evolution,

<sup>41</sup> A. B. Hollingshead, *Ecol. Monogr.*, 10: 354-366, 1940.

however, we are dependent upon a long individual life cycle and a long individual process of learning. Each human must spend a third of his life at least acquiring certain effective social traits and we must also train a large proportion of our population to function mainly for social coordination. What is most obvious at the present time, although the larger interdependent, international, world society is already highly integrated through commercial, transportative and communication systems, we have not yet been able to adequately master destructive national and class competition. It is our hope that the discovery by the social scientists of the mechanisms and details of cooperative social organization will ultimately enable mankind to evolve beyond this present phase with its inefficiency and misery. Within insect societies social intraspecific class or colony wars are practically nonexistent and this difference from men is correlated with the slow evolution of germinal heredity of social traits among insects and the rapid evolution of social heredity through symbols and learning among men. It is to be expected that our aggressive tendencies will be directed into constructive channels leading to greater social and biological efficiency in time.

The basic forces which have led to convergence in social patterns of insects and men and the parallelisms between individual organisms and societies remain to be explained. We have seen that the ecological principle of natural selection has guided evolution into adaptive channels. We have also noted that environmental fluctuations are limiting factors in the distribution of species. Not only do organisms acquire energy, reproduce their kind and defend themselves against predators and parasites, but they maintain themselves in the environment to which they are adjusted. This necessity for maintaining ecological position is seen particularly in the myriad adaptations for attachment and locomotion. Ecological position not only involves a relatively uniform physical environment, but also a relatively stable source of energy,



a relative security from enemies and a relative accessibility of cooperative individuals. Competition within favorable habitats has produced a selective orientation toward more efficient adaptations to the physico-chemical and biotic factors in the environment. In addition, adaptive radiation from more favorable primitive environments has occurred in all the main plant and animal stocks. Because of competition for limited necessities within favorable environments, there is an added selective force favoring mutations which would lessen this competition.<sup>42</sup> Most often adaptive radiation occurred by means of an internal control over an external fluctuation. Living protoplasm maintained a relatively constant composition of water, ions and metabolic materials in the face of environmental fluctuations of these materials. The naked cell, however, lived in less optimal conditions than did the cell in a group. Through division of labor and coordination between cells, the external environment of the single-celled organism became the internal environment of the multicellular organism. The evolution of the controlled cellular environment has reached a truly astonishing development of stable equilibrium and controlled periodicity in the physiological constants of higher plants and animals.

In spite of such successful evolution, however, there were still fluctuations in the external environment of the multicellular organism that seriously limited its existence. Aggregating forms could bring the external environment under partial control. Two trends of population evolution emerged in the development of greater living efficiency by means of natural selection. Ecological communities developed with interspecific integration which produced a partial environmental control and a relative environmental stability for the individual organisms. In addition to this type of organization, a second evolutionary trend directed the development of intraspecific popu-

<sup>42</sup> G. K. Noble, "The Biology of the Amphibia." xiii + 577 pp. p. 83. New York: McGraw-Hill Book Company, 1931.

lation groups and progressed toward greater and greater control of an otherwise fluctuating external environment. Sexual adjustments brought a balance between hereditary conservatism and variation. Reproductive adaptations tended to control the environment of the young during early developmental stages (*i.e.* the egg and the uterus). Familial integration controlled the environment during the later stages of ontogeny (*i.e.* nests, parental feeding, parental defense) and the family as a biological unit of great importance became established. Selection in these cases was not working alone upon the individual organism. The population was the unit of selection, much as the population of cells composing the multicellular individual was selected as a coordinated unit. A logical explanation of the evolution of such familial adaptations as mammary glands is impossible by means of natural selection of individually fit multicellular organisms. The family unit thus has attributes of the organism for the simple reason that the basic forces guiding the familial and organismic integration are similar.

But the end was not reached in the family organization. More complex units could more thoroughly control the external environmental fluctuations. Nests and shelters could be made more adequate through the cooperation of many specialists, enemies could be more successfully repulsed, food could be brought under cultivation (*i.e.*, fungus-growing social insects and human agriculture), reproduction could be more adequately adjusted to the population needs, hostile environments could be invaded. Men and insects have accomplished these feats through societal systems and the fundamental forces which have guided social evolution have some identity even though the germinal stocks are widely divergent.

Competition plays a tremendously important rôle in evolution, but the survival of the fittest does not always mean the survival of the strong, the predators, the parasites, or even the adequately defended organisms. Fit-

ness may mean cooperation for mutual benefit both between species and within integrated intraspecific populations as well as between parts of the individual organism. Cooperation between the parts of all living organismic units is a fundamental biological principle. Cooperation is not an end in itself, but is the means to the end. Cooperation is one of the important adaptive mechanisms with survival value which results in the attainment of an internal and external equilibrium. Natural forces guide the biotic unit toward the control of the protoplasmic environment which is brought closer to the optimal point for the organism concerned. The optimum, with our present knowledge of physiology and ecology, is often a rough approximation. Optimal conditions at one stage of development are not optimal at other stages. The optimum for one organismic function is not necessarily the same for other functions. There are regular and irregular cycles both in the organism, supraorganism and environment which are reflected in periodic phenomena, special adjustments and a compromise or balance between complex and sometimes antagonistic forces. Balanced equilibrium is thus characteristic of the units of each organismic level from viruses and cells to the social groupings and ecological communities and the division lines between these biological entities are not sharp.

The way in which the social supraorganism may interdigitate with the biotic community is illustrated by the social parasites and commensals. Just as numerous animal and plant species are incorporated into human society, the social insect colony is an interspecific ecological community consisting of numerous species of plants and animals adjusted both parasitically and symbiotically to the internal environment of the supraorganism. Cleveland<sup>43</sup> has shown that the wood-eating roach and termite communities were fundamentally

<sup>43</sup> L. R. Cleveland, *Mem. Amer. Acad. Arts and Sci.*, 17 (2): x+1-342, 1934.

functional adjustments promoting an efficient cooperation between the wood-eating insects and their symbiotic cellulose-digesting intestinal protozoa. In order that the molted individual could become reinfected with protozoa, it was necessary for such an individual to live in a family or social community. Thus evolution has resulted in an integrated, balanced, biological system incorporating organisms of various species and various organismic levels, in its entirety exhibiting dynamic equilibrium between its parts and with its external environment.

Of what value are such generalizations? It seems to me that significant relationships between diverse phenomena indicate more universal and thus more fundamental principles thereby enabling us to arrange biological attributes in a more logical and scientific order. Chronological order may help us to detect causative factors more easily and to predict events with greater accuracy. Factorial analysis and the observation of the activity of whole synthetic systems produces knowledge of the guiding forces in the world in which we live. As knowledge grows, however, we become more aware of the great gaps in our factual experience and classificatory systems. We thus become more sensitive to our ignorance and more energetic in the accumulation of pertinent data. Through the advancement of science we gain a greater control over our complex internal, external and social environment, thus finding ourselves in harmony with the forces of progressive evolution which have been directing life since its origin.

## THE INHERITANCE OF EGG PRODUCTION IN THE DOMESTIC FOWL<sup>1</sup>

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THE problem of inheritance of egg production in the domestic fowl has attracted considerable attention, particularly because of the practical implications of the subject. As is the case with many other characters of economic import, the progress towards the solution of the problem has been rather slow. In fact, to date only two significant landmarks in the history of investigations in this field can be pointed out. The first of these is a series of papers by Pearl (1909 *et seq.*) which constituted the initial fruitful investigation of the question, while the second is the methodological innovation introduced by Goodale (1918). The voluminous literature on the subject built up since (*vide* Jull, 1940), deals with many important points, but practically in all cases they are elaborations and refinements of what may be called the Goodale principle.

### MEASUREMENT OF THE ANNUAL RECORD

The first step accomplished by Pearl consisted of the recognition of egg production as a heritable character based on Mendelian segregating units. Because of the comparatively low standard of productivity of most flocks at the time of Pearl's work, he found the egg production during the winter months to be a reliable criterion of the inherited ability to produce eggs. At the present time, however, winter production can no longer be used as the sole differential between superior and inferior layers. The distribution of egg production during approximately the first 18 months of life is considered a more adequate

<sup>1</sup> The writers wish to express their indebtedness to Dr. J. L. Lush of the Iowa State College for his valuable advice in connection with the determination of the degree of heritability.

criterion of measurement of laying ability. In breeding practice, the production during the 365 days immediately following the first egg laid by a bird is often held to be synonymous with the annual record. This period based on a temporal scale is, of course, entirely arbitrary from the biological point of view. The biological laying year used to designate the period of time from the first egg to the first complete molt has probably a better foundation, but it presents some difficulties in practical application. The difficulty lies in the fact that annual replacement of yearling hens in the laying houses by pullets coming into production has to be made, for the sake of efficient management, not individually but *en masse*. Consequently, the birds with extremely long biological laying years may be removed before molting, so that their biological laying-year records remain incomplete. As a compromise measurement the production from the date of first egg to a fixed date in the fall of the second year of life is often used. In the material presented in this paper, for instance, production to October 1 of the second year of life is referred to as the annual production.

#### THE COMPONENTS OF THE ANNUAL RECORD

The contribution made by Goodale (1918) consisted of breaking down the annual record into its component parts. He considered annual production as an integration of a number of characters. Similarly, Hurst (1921) a few years later dissected the annual record into fall, winter, spring and summer production and attempted to assign special Mendelian factors for each. Such procedure not only involves arbitrariness of selection of seasonal limits but can readily resolve itself into absurdity should the process be extended by further subdivision into still shorter periods until oviposition on each day of the year is considered to be determined by the presence of a specific gene.

Goodale's original premise, on the other hand, is very sound. Though not stated in precisely this manner, the

concept expounded by him visualized annual egg production as a function of the time during which the bird is laying and of the rate at which the bird lays during that period. The time factor itself can be resolved into the time of commencement of egg production (age or date at sexual maturity), the time of onset of the molt which normally is coincident with cessation of production (age or date at last egg or persistency) and any periods of interruption of lay between the two above points on the time scale (winter pause or pullet fall molt, broodiness). By using this principle, selection for the total number of eggs produced in a year could be supplemented by selection against deficiencies with respect to these component characters so that the lack of desirable characteristics in one mate could be compensated by a specific superior trait in the other.

The formulation of Goodale's hypothesis was shortly followed by attempts to place the inheritance of these characters on a simple Mendelian basis. Hays, in a lengthy series of publications (1924 *et seq.*) suggested, on empirical grounds, that one or two genes are involved in the genetics of each of the following traits: (1) age at sexual maturity, (2) winter pause, (3) broodiness, (4) persistency, and (5) rate. Most of the other investigators have not entirely adopted Hays' interpretation, since it was obvious that the genetic picture had been greatly oversimplified. For instance, Hays himself was not able to eliminate all the undesirable recessive or even dominant characters from his flock after 16 years of selection (Hays and Sanborn, 1934), which should have been a comparatively simple procedure were only one or two genes concerned in their expression. However, the best that has been offered in lieu of Hays' theory was to invoke a larger number of genes responsible for the expression of each of the component characters. Munro, Bird and Hopkins (1937), at least by implication, rejected Goodale's principle altogether and postulated instead the existence of several hundred "protective" genes enabling birds pos-



sessing them to withstand adverse environment to produce the given number of eggs.

The fundamental misconception in dealing with Goodale's principle has been the assumption that the component characters are genetic entities, with a smaller or larger number of specific genes exercising an effect on their expression. An alternative point of view is that the characters contributing to the egg record are not necessarily independent phenotypic expressions of particular genes. Thus it may be suggested that such characters are purely arbitrarily defined observables which in combination account for the variation between birds in their annual production.

This point of view appears to be biologically sounder than that of Hays and is just as fruitful from the standpoint of practical breeding accomplishments. Any number of characters may be selected, so long as they answer three criteria:

- (1) The characters chosen must contribute to the variance of the annual egg production.
- (2) They must preferably be independent of each other.
- (3) They must show genetic variability.

The definitions and methods of measurement of the characters chosen may be modified so as to maximize their contribution to the annual record and their genetic variability and to minimize interaction between them. It has been the effort of several investigators, whether or not they held to the point of view expressed here, to determine what particular characters answer best the criteria propounded. Gradually characters suggested by Goodale have been defined and re-defined until the first two criteria have been satisfied. The purpose of the present contribution is to examine these characters with respect to the third criterion, that of genetic variability and thus to complete steps necessary for the formulation of a theory of inheritance of egg production built upon Goodale's original premise.

## STUDIES OF THE COMPONENT FACTORS

Numerous reports are available on the correlation between annual egg production and each one of the component factors. For instance, with respect to maturity, Knox (1930) review 18 separate papers demonstrating the influence of sexual maturity on the variation in the egg record. The correlations between the other components and annual production have been similarly investigated, though not on as extensive a scale (*e.g.*, Hays and Sanborn, 1927; Knox, Jull and Quinn, 1935; Lerner and Taylor, 1937a). The magnitude of the contributions made by each of the factors varies, but there is little doubt that maturity, persistency, pause, rate and broodiness all contribute to the annual record. The way in which these factors are measured, of course, determines to a considerable extent the size of the correlation coefficients reported. The total amount of variability in the annual record accounted for by the variation of the components has been reported by Hays and Sanborn (1927) as about 75 per cent. by Lerner and Taylor (1937a) as 55 to 90 per cent. (only maturity, persistency and rate being considered), and by Knox, Jull and Quinn as 70-80 per cent. (including date of hatch as an additional independent variable).

The second criterion cited, that of independence between the measurements of the component factors, has proved a stumbling block for a considerable time. The first elaborate attempt at re-definition of Goodale's original variables was made by Knox, Jull and Quinn (1935) who, by using what in effect amounted to coefficients of alienation, determined which combination of individual measurements gave the highest multiple correlation with egg production. Their definitions, however, were not entirely adequate. For instance, rate was expressed by them as the percentage of production to March 1, a measurement which in reality combines two independent characters: net rate and winter pause (Lerner and Taylor, 1936). However, as a result of these and other studies it is possible to define at least tentatively the com-

ponents involved (the years refer to the publications by the present writers):

- (1) Maturity—age at first egg (1937b);
- (2) Persistency—date of last egg (1937b and c);
- (3) Rate—per cent. production, calculated by excluding pausing and broody days from consideration (1936);
- (4) Winter pause—presence before March 1 of non-productive periods of seven or more days' duration (1939);
- (5) Broodiness—manifestation of broody behavior.

The third criterion noted refers to the genetic variability in these characters. That some degree of hereditary control is involved in all of these has been shown on many occasions. A single reference may be mentioned for each factor: maturity—Warren (1934); persistency—Lerner and Taylor (1937a); rate—Hays (1932); winter pause—Lerner and Taylor (1939); and broodiness—Hays (1940). However, no estimates of the actual degree of heritability have been made heretofore. The present paper makes an attempt to fill this gap in our knowledge of the subject.

#### MATERIAL AND METHODS

The material used in this study was obtained from the March- and April-hatched Single Comb White Leghorn flock of the University of California, including birds selected for and against desirable production characters as well as those selected for susceptibility to disease, size, differential shell thickness and other factors not immediately connected with annual records. Four series of pullets hatched in successive years were used, and in each all full-sister families of four or more birds were selected. A further prerequisite for inclusion in the analysis was that the dam and the sire were to have been hatched in the same year and to have a minimum of four full sisters also hatched in that year. This method of selection provided 117 families of daughters, including 905 pullets, which originated from 36 different sires and 109 different dams. A total of 1,480 females, including daughters, dams and the sisters of parents, were used in all. This figure does not include the cases of duplica-

tions where the daughters of one series were dams or aunts in another. There were five series of birds all told, since the earliest series contained only the sire's and the dam's families and the latest series only the daughters.

A number of statistics for each of the families were calculated. At the same time the constants for the same variables for all females hatched in each year were computed (Table 1). The raw data for each family were

TABLE 1  
PRODUCTION CHARACTERISTICS OF THE BIRDS USED

Series	Total number of birds	Median age at first egg, days	Per cent. non-pause	Per cent. high rate	Per cent. persistent	Per cent. viability	Average maximum egg size, grams	Average production of survivors, eggs	Production index, eggs
K	230	187.2	43.2	47.1	61.8	48.7	58.5	238.5	154.7
L	305	180.3	33.0	57.0	63.8	59.7	60.7	226.5	166.4
M	433	176.3	35.7	56.7	40.0	49.9	60.0	223.9	154.3
P	299	176.8	29.6	55.8	44.1	36.8	58.4	217.6	129.6
R	213	172.9	20.1	74.4	55.8	58.2	60.6	235.8	176.3
Total	1480	177.5	32.7	58.0	51.9	50.3	59.7	227.8	155.0

then converted into deviations from these constants for the respective year of hatch. In this manner, environmental inter-year variation to which all birds hatched in the same year were subjected was removed. Similarly, the effect of any changes in the genetic make-up of the population between years was excluded. Since the members of the different families were not segregated at any time since their emergence from the incubator, it follows that the intra-year environmental effects are to be preponderantly found within rather than between families. The procedure used in the analysis deals exclusively with differences between families so that the intra-year environmental variation may be neglected.

The variables investigated, in addition to the component factors of egg production already enumerated, included such characteristics as egg size and viability, both important in commercial egg production. Broodiness was not included in this analysis, because its level has

been very low in the flock studied. Thus, there were eight factors not weighted for differences in the number of birds per family studied altogether:

(1) Sexual maturity, expressed as the median age at first egg for each family (Lerner and Taylor, 1940).

(2) Winter pause, expressed as the percentage of non-pausing birds (see definition above) in a family.

(3) Rate, measured by the percentage of birds in a family which showed a high rate of production, as judged by the records in the winter months (see Taylor and Lerner, 1938, for full description of this measurement).

(4) Persistency, expressed as the percentage of living birds in production on October 1 of the second year of life (Taylor and Lerner, 1938).

(5) Viability, as judged by the percentage of birds alive at approximately five months of age still living on September 25 of the second year of life.

(6) Egg size, expressed as the mean monthly maximum egg size for the family (Taylor and Lerner, 1938).

(7) Annual production of survivors to October 1 of the second year of life.

(8) Production index, representing the average number of eggs laid by each family on the basis of the number of birds housed at about five months of age.

#### DETERMINATION OF THE DEGREE OF HERITABILITY

The method best recommended for the determination of the degree of heritability is the intra-sire regression (Lush, 1940). However, it is not suitable for the material at hand, because in most cases here the characters dealt with have only a presence or absence value in the dam. Hence the following procedure was adopted. Simple correlation coefficients were computed between the values for the sire's sisters and sire's daughters, the dam's sisters (exclusive of the dam) and the dam's daughters, and between the values for the sire's sisters and the dam's sisters, again exclusive of the dam herself. In some cases certain of the families had to be omitted from consideration, where mortality did not permit some of the values to be calculated. For instance, if all the dam's sisters died before their persistency could be determined, the family had to be eliminated from the calculations involving persistency. In each case the daughters were included only where the values for sisters of both parents were available. In such manner the number of

families used for each factor varied from 100 to 117. The particular numbers, together with the correlation coefficients, are presented in Table 2.

TABLE 2  
SIMPLE CORRELATION COEFFICIENTS

Character	Number of families	Correlation coefficients		
		Sire's sisters-daughters	Dam's sisters-daughters	Sire's sisters-dam's sisters
Maturity .....	117	0.295	0.168	0.087
Winter pause .....	116	0.184	0.172	0.260
Rate .....	113	0.253	0.290	0.372
Persistence .....	108	0.090	0.123	-0.011
Viability .....	117	0.257	0.012	0.158
Egg size .....	112	0.344	0.424	0.309
Survivors' production ..	100	0.293	0.231	0.247
Production index .....	117	0.294	0.233	0.384

The theoretical coefficient of correlation between individual aunts and nieces on the basis of random mating, without epistasis and  $p = q$  with complete heritability, is 0.25 in the case of autosomal genes without dominance. With complete dominance the value of the coefficient under the same stipulations is 0.1667. In the case of sex-linkage, the sire's sisters-daughters correlation in either instance is 0.25, while that between dam's sisters and daughters is zero (Hogben, 1932 and 1933, making provision for the difference between mammals and birds with respect to the heterogametic sex).

On the basis of these figures it is easy to see that the determination of the daughters' values by those of the two types of aunts combined (the square of the multiple correlation coefficient) is 12.50 per cent. in the case of autosomal inheritance without dominance; 5.56 per cent. with dominance, and 6.25 per cent. in the case of sex-linkage with or without dominance.

Under conditions of random mating the comparison of the observed figures with these theoretical figures should indicate the degree of heritability<sup>2</sup> of the characters in

<sup>2</sup> The degree of heritability as used here refers to that portion of the variance between families which is attributable to genetic effects. It should be clear that the degree of heritability between individuals in Lush's (1940) sense is higher than our figures, because it includes the intra-family genetic variation as well as the inter-family genetic variation considered here.

question. However, the data used here do not consist of individual values but of averages. Dr. J. L. Lush has pointed out to us that the effect of averaging is to increase the theoretical correlations. Because of the effect of the correlation between full sisters (both in the aunt family and in the niece family), the aunt-niece average correlation in the extreme case, that of autosomal inheritance without dominance, approaches 0.50 as a limit as the size of the families increases. Under these conditions the theoretical multiple determination rises to 50 per cent. As indicated in Table 2, most of the matings in the material at hand were assortative to some extent. There is, however, considerable variation in this respect in the different characters. The maximum degree of consanguinity represented is in the case of two full brother  $\times$  sister matings out of a total of 117 matings. In order to calculate the increase in genetic variability due to the non-randomness of matings, Wright's method of path coefficients as outlined by Tolley (Elliott, 1927) was used.

#### THE DEGREE OF HERITABILITY OF THE COMPONENT FACTORS

Table 3 presents the results of this analysis, showing, in successive columns, the total determination of the daughters' values by both types of their aunts, by their

TABLE 3  
COEFFICIENTS OF DETERMINATION\*

1 Character	2 Total determi- nation (R <sup>2</sup> )	3 Direct determi- nation by sire's sisters	4 Direct determi- nation by dam's sisters	5 Joint determi- nation
Maturity .....	0.1075	0.0798	0.0207	0.0070
Winter pause .....	0.0503	0.0223	0.0176	0.0104
Rate .....	0.1089	0.0284	0.0519	0.0286
Persistency .....	0.0236	0.0084	0.0154	-0.0002
Viability .....	0.0669	0.0684	0.0009	-0.0024
Egg size .....	0.2293	0.0554	0.1225	0.0514
Survivors' production ..	0.1126	0.0631	0.0285	0.0210
Production index .....	0.1033	0.0576	0.0199	0.0258

\* R<sup>2</sup> at P = 0.05 varies from 0.0515 to 0.0625, depending on the number of families.



paternal aunts directly, by the maternal aunts directly, and the joint determination. It may be seen that with the clear-cut exception of persistency and the border-line case of winter pause all of the total figures are significant. In comparing the relative contributions of the sires and the dams to the variability of the daughters, it is possible that previous selection has had a differential effect on the variability of the sisters of each of the parents. There is no reason to suspect, however, that in this population such effect would be of any great significance.

In the case of maturity, the operation of sex-linked genes is suggested by the considerable excess of the figure in column 3 over the one in column 4. It is highly likely that similar excesses for the survivors' production and the production index are due to the sex-linked genes for maturity. These have been noted earlier by Warren (1934) and by Hays (1936) within the Rhode Island Red breed.

The contributions made by the paternal and maternal aunts to the winter pause of the daughters are about equal. In the case of rate, the determination on the dam's side is somewhat greater than on the sire's side, but not necessarily significantly so. The measurement used for persistency does not appear to represent adequately any of the possible genetic variability in this material. The reason for this is obscure, since date of last egg has been shown previously (Lerner and Taylor, 1937b) to exhibit significant variability between sires. Neither is it clear why viability of the dam's sisters is not correlated with that of the dam's daughters. The two measurements of production (survivors' production and production index) are the result of integration of the first four and five characters respectively. Since they do not operate in a direct additive fashion and, in fact, may in some instances run counter to each other in their effect on egg production, the total determination in the case of the latter is not necessarily equal to the sum of the determinations of the component characters. The

value reported here for survivors' production approximates rather closely the estimate of the proportion of genetic variability in records of Canadian egg-laying contests made by Munro (1936).

The considerable excess in column 4 over column 3 in the case of egg size might indicate either a maternal effect or an effect due to factors carried on the heterochromosome. The two possibilities can not be distinguished from the material at hand. It is curious that indications of a similar effect have been noted with respect to some other egg characteristics such as shell thickness (Taylor and Lerner, 1939) and percentage of firm white (Lorenz and Taylor, 1940).

For the purpose of estimation of the degree of heritability the figures in column 2 of Table 3 may be divided by one of the theoretical figures cited above. To be on the conservative side the minimum degree of heritability may be determined by using the highest of these as the denominator. This is the aunt-niece correlation on basis of autosomal inheritance without dominance, assuming the number in each family to be indefinitely large (0.50). This would obviously lead to an underestimate of the degree of heritability, since (1) the number per family averages less than eight, (2) there are sex-linked factors involved in some cases, and (3) some of the genes may be dominant. The quotients thus obtained appear in Table 4. They represent then the minimum heritability in this

TABLE 4  
MINIMUM ESTIMATES OF THE DEGREE OF HERITABILITY BETWEEN FAMILIES

Character	In actual population, per cent.	Under random mating, per cent.
Maturity .....	21.5	20.1
Winter pause .....	10.1	8.0
Rate .....	21.8	16.1
Persistency (not significant) .....	4.7	4.8
Viability .....	13.4	13.9
Egg size .....	45.9	35.6
Survivors' production .....	22.5	18.3
Production index .....	20.7	15.5

population. It is also possible to estimate the degree of heritability were random mating practiced. The assorta-

tive mating in this population is largely due to the formation of non-interbreeding families. This, of course, increases the proportion of genetic variability between families. In random matings the joint contributions would not appear and division of the sums of the direct contribution by the theoretical multiple correlation would give the desired data, also shown in Table 4.

#### CONCLUSIONS

It is clear from these data that in the flock studied there still is a reserve of genetic variability in all of the characters studied, with the exception of persistency as here measured. This reserve is of sufficient magnitude to make selection on the basis of progeny testing an effective tool in improving production characteristics (see Wright, 1939). In the case of persistency, it is possible that a different measurement than the one used here need be selected.

It may be then considered that the present paper demonstrates the application of the third criterion to the Goodale principle. On the basis of the data presented here, and those referred to in the course of the discussion, it is possible to state that egg production records are resolvable into independent observables with high genetic variability significantly contributing to the variation in egg production. It is obvious that observables such as these may be selected arbitrarily for any other production complex as well. For successful and efficient application in breeding practice they have to answer the criteria listed, and so long as they do, can be used advantageously in improvement programs, irrespective of their biological basis.

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## SPECIALIZATION AND EVOLUTION

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HIGHLY specialized animals have always aroused man's natural interest in the bizarre and unusual in nature. Biologists when writing text-books and popularizations have utilized this interest, witness the frequency with which dinosaurs, birds of paradise, giraffes, whales and other remarkable animals are figured and mentioned in such works. The role of such specialized forms in evolution has also received much attention. Most zoologists seem to be in agreement concerning this question. Their conclusions may be summarized briefly as follows: although specialized animals are interesting and, in the case of such forms as the neutral castes of social insects, almost baffling examples of the potency of natural selection and other evolutionary factors, they represent extreme end-products of evolution which have or will become extinct more quickly than their less specialized relatives whenever conditions change, however slightly. For this reason it is generally believed that specialization has been of little importance in evolution, since during periods of geologic upheaval and great environmental change only generalized forms have survived. Furthermore, the belief is widely held that specialization runs its course, so to speak, and that specialized forms become, as it is variously expressed, "senescent," "implastic," "static," "over-specialized" or "genetically fixed" and hence incapable of further change or adaptation or of playing a further part in evolution. This line of thought is apparent in the frequently encountered assertions that man as a species will have a short future history because he is too specialized for further extensive genetical modification or evolution to be possible. The present note is written to present the opposite point of view, namely, that many of the most important advances in evolution have been the

result of specialization and that modern knowledge of genetics suggests that specialized animals are in general even more likely to undergo further genetical modification than are unspecialized ones.

#### SPECIALIZATION AND SURVIVAL

We may define a (morphologically) specialized animal as one having one or more organs or structures greatly modified or developed as compared with other related species. Sometimes an entire group is specialized and comparison must be made between groups. As regards probability of survival under changed conditions, it is possible to distinguish two types of specialization. The first is that found in a species which is specialized in such a manner as to make its existence dependent upon the continuance of a peculiar environmental niche or sequence of events. The inter-dependence of the yucca moth (*Pro-nuba*<sup>1</sup>) and fig wasp (*Blastophaga*) with the plants which they pollinate are classic examples. If either plant or insect were to become extinct, the other member of the partnership would become a victim of its own specialization. Host specific parasites, especially those which pass successive stages in different hosts, would also seem to be specializing in a way which imperils their survival.

Consideration of such examples as the preceding is responsible for the belief that specialization *per se* leads to an evolutionary *cul de sac* and eventually to extinction. Such a conclusion, however, ignores the numerous forms which are equally specialized morphologically and yet are as well or better equipped for survival than more conservative species. The extreme specialization of whales has permitted them to utilize an environment which is more widespread and less subject to change than the habitats of terrestrial mammals. Birds, as Huxley remarked, are only "glorified reptiles," but they seem better able to survive than their less "glorified" reptilian relatives. Relic survivors of nearly extinct groups are often highly

<sup>1</sup> Now *Tegeticula*.

specialized. In some cases at least, it seems probable that such species have survived because they were specialized. This would seem to be true of the monotremes and many primitive insectivores which are highly specialized for unusual aquatic or subterranean niches. Simpson (1941, p. 17) has written of the king-crab, a member of a group which has flourished almost unchanged since the Triassic, "Far from dooming it to extinction, its specializations seem almost to be a recipe for group immortality." Nor can it be assumed that major changes of environment will necessarily place specialized forms as a group at a disadvantage. Bats and birds, for example, would probably find the mobility which specialization has conferred upon them advantageous under such conditions. Even of species which seem to be jeopardizing their survival by specialization for restricted or marginal habitats, a certain number would probably be benefited by changes of environment. A catastrophic rise in temperature, for example, might be fatal to all life except those algae which are specialized for life in hot springs.

#### SPECIALIZATION AND EVOLUTIONARY ADVANCE

One of the puzzling features of historical evolution has been the apparent suddenness with which many major groups seem to have appeared and the correlated rarity of "missing links." So formidable has this difficulty appeared to some students that they have concluded that new species and even major groups appear instantaneously as the result of radical "systemic mutations." Such a point of view is at variance with the known facts of geographical variation and genetics and introduces a pre-Darwinian mystical or miraculous aspect into evolution. Is it not possible that the difficulty arises from the fact that new major groups have often evolved from highly specialized (and hence often rare) forms? The rarity of missing links and the apparently great gaps which separate many major groups are both understandable if it is assumed that the transition from one major



group to a derived one is often effected by one or a few very aberrant and specialized forms.

The discoveries of paleontologists have supplied much evidence which seems to support this suggestion. It was, for example, a very specialized group of fishes which acquired the ability to breathe air and walk on their fins and thus gave rise to the amphibia and eventually to all the higher vertebrates. By way of contrast, sharks, a generalized and conservative group, have not changed greatly since the Devonian except to degenerate somewhat. Again, one specialized branch of the Reptilia gave rise to the birds and another to the mammals. Meanwhile reptilian groups with less of a tendency towards specialization, such as *Sphenodon* or even the more primitive families of lizards, have remained essentially unmodified. Two of the most specialized orders of mammals, bats and whales, must have evolved as a result of specialization which continued until the attainment of flight in the bats and independence of land in the whales suddenly provided "new worlds to conquer." Although at that time the ancestors of both groups must already have been highly specialized for a long period, there is no evidence that this had reduced their potentialities for further modification and evolution. Instead both underwent a rapid adaptive radiation until the opportunities of the new medium had been exploited.

An illustration of how specialization might again lead to an important evolutionary advance is supplied by Raven's recent studies (1939a, -b) of the anatomy of the peculiar ocean sunfishes of the family Molidae. In this family almost every structural feature of ordinary fishes has been transformed and specialized. These modifications have produced an amazing disc-shaped fish in which the *lateralis* musculature, which comprises 90 per cent. of the weight of a typical fish, has been completely lost. The locomotor function usually performed by these muscles has been taken over by the erector and depressor muscles of the dorsal and anal fins, which have become

greatly hypertrophied. Most interesting, then, was the discovery of a rare and most-modified member of the Molidae, *Ranzania truncata*, in which the body form has become secondarily elongated to again approach that of an ordinary fish. It is entirely conceivable that its new pattern of musculature might give *Ranzania* a competitive advantage over other fishes. If this should happen, many of the latter would be replaced by Molids, which would rapidly, phylogenetically speaking, differentiate into a variety of forms adapted to various ecological niches.

The foregoing considerations make it appear probable that it has frequently been specialized forms which in the past have and in the future may be expected to give rise to new groups of major rank. For it is only in highly specialized forms that the possibility exists of stumbling upon, so to speak, entirely new structures or processes, of which a few from time to time will prove to be of revolutionary importance.

#### SPECIALIZATION AND GENETICS

Evolution might almost be defined as a process by which originally simple organisms have become increasingly modified and complex in structure and function. Partial reversals of this trend may be observed in so-called degenerate forms, but nevertheless all the members of such advanced groups as insects or mammals are amazingly complex when compared with representatives of lower and broadly speaking ancestral Phyla. The implications of this trend, it would seem, are overlooked by those who believe that specialization leads to genetic fixation. Specialized forms are those in which the usual evolutionary trend towards increasing complexity has been somewhat accelerated. On *a priori* grounds it is more logical to suppose that they will continue to change faster than their more conservative relatives than to postulate the opposite.

Dobzhansky's recent summary (1941, especially Chaps.

5, 6, 10) of genetics as related to speciation and evolution gives no support to the belief that specialization decreases a species' potentialities for further change. He points out that each species (or more or less isolated population within a species), as a result of the selection exerted by the particular environment in which it lives, tends to reach an adaptive peak in which the effects of such dynamic factors as mutation pressure, population size and migration pressure are balanced. If any of these factors, including the environment, changes or becomes dominant over the others the rate of evolution will thereby become greatly accelerated or retarded. There is reason to believe that in highly specialized species such an unbalanced condition will exist more frequently than in others. Thus the total populations of specialized species will often be small, since they are frequently adapted to an unusual and restricted type of environment. In such populations, as Sewall Wright and others have proved theoretically, natural selection becomes largely non-effective. Favorable genes may be lost and neutral or deleterious ones fixed merely by chance genetical recombinations. The result is a non-adaptive population which is undergoing rapid genetic change. This will often lead to extinction, but sometimes one of the new genotypes, which has been produced by chance, will prove to be "pre-adapted" to a new, unoccupied environmental niche. When this occurs, an increase in numbers will follow and the modified species will reach a new adaptive peak adjusted to its changed habitat.

The acquisition of tusks in the Proboscidea may have resulted from the operation of such processes in a numerically small, specialized group. Apparently the tusks had their origin in a mutation which prevented occlusion of the incisor teeth. Although this mutation was probably at first unfavorable, at least one population in which it had become established through chance genetical fixation was able to survive. Eventually the tusks became useful in fighting and perhaps in feeding. They

then came under the influence of natural selection and finally only those species in which they were well developed survived.

It is possible that specialization tends to change the rate of evolution of a species in other ways also. Some have suggested that such groups as the birds of paradise, in which almost every species is characterized by peculiar specializations, may have acquired an unusually high rate of mutation by natural selection. The mating habits of this family confer an advantage upon specializations which permit females to immediately recognize males of their own species. Until more research has been accomplished in population genetics, it is not profitable to speculate further. It is to be hoped that students of this promising subject will give especial attention to the study of evolutionary patterns in highly specialized species.

#### SPECIALIZATION AND CLASSIFICATION

Some systematists have incorporated their beliefs on the role of specialization in evolution into the classifications which they have proposed for various groups. Wetmore, for example, in his revised classification of the Class Aves (1940) has placed the relatively generalized sparrow family at the apex preceded by more specialized groups because the latter are "... assumed now to be more or less static and fixed and therefore should stand at the side" (p. 2). However, if such a procedure were adopted for animal classification in general, it would be necessary to place the generalized protozoans, etc., at the apex, preceded by all the specialized, derived groups!

A classification can not express everything, and it is equally inadmissible to put a specialized group above others merely because it is specialized. The important thing is to put ancestral groups below derived groups which evolved from them. Some members of ancestral or lower groups may, of course, survive to exist side by side with the derived ones. The duck-billed platypus is a uniquely specialized mammal, but as regards those par-

ticular specializations of the pectoral girdle, reproductive system, etc., which led to all the modern mammals it is very generalized, almost reptilian. This shows it to be a surviving relic of a group ancestral to the marsupials and placentals and it is correctly placed below them in accepted classifications.

It is here assumed that a phylogenetic classification is the goal desired. Strenuous objections from time to time are brought against this assumption by those who believe that animals should be classified according to the totality of characters which they have in common, regardless of relationship. As Dobzhansky (*op. cit.*, pp. 362-365) has shown, this conflict is more apparent than real, first because phylogeneticists must perforce usually infer phylogenies from the possession of common characters plus (sometimes) sequence in time, and second, because the assumption that phylogenetically related animals will almost always have more in common than those not so related appears to be valid. It might be pointed out that this last assumption receives partial proof from breeding experiments which show that strains having close blood (phylogenetic) relationship are as a rule more alike than more distantly related strains.

#### SUMMARY

Although specialization sometimes leads to extinction, it often confers an advantage upon a species in its struggle for existence. There is considerable paleontological evidence to indicate that new groups have often evolved from specialized members of a lower group. The suggestion that specialization has played an important role in evolution is not at variance with present knowledge of genetics, and receives some support from current theories of population genetics. The relation of specialization to classification is discussed.

I am greatly indebted to Professors William K. Gregory and Theodosius Dobzhansky and Dr. Ernst Mayr for criticism of this paper.

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## EDMUND B. WILSON—AN APPRECIATION

DR. H. J. MULLER

*(Continued from page 37, January-February, 1943, issue)*

### UNITING CYTOLOGY WITH MENDELISM

WILSON's remarkable appraisal of the problems confronting all research, which was reviewed in the preceding section, was published four years before the three almost simultaneous epochal announcements of the rediscovery of Mendelian heredity. The stage had indeed been set, and this discovery was no longer too far ahead of its time. Both Correns and de Vries very soon offered a chromosomal interpretation of their findings. This, however, was based on an assumed random assortment of conjugating chromomeres which—though it contained the germ of the crossing over theory—departed in some ways too far from the then ascertainable facts of chromosome behavior; consequently it did not serve as the main route by which the connection of cytology with Mendelism was made. It was reserved for Sutton, working as a student of synapsis under the guidance of Wilson, to confirm in his own preparations Montgomery's surmise of chromosome homologies, and by its means to show that the visible behavior of the chromosomes, so far as known, was such as to afford an explanation of both the first and second Mendelian laws—though the chromosomal application of the second law (that of random assortment) was as yet only a very probable inference, based on the visible separateness of the pairs. Wilson at once (1902) came to the support of Sutton's conclusions, while at the same time calling for more extended study of the cytological phenomena concerned.

In the same year McClung—who had started in cytology as a student of Wilson's only three years before—called attention to the fact that the unpaired chromosome (later called the "X" by Wilson) long known to exist in the males of some arthropods might provide an



explanation of sex determination. Confirmation of this penetrating inference was delayed by faulty observations of some other workers and also by apparent contradictions occasioned by McClung's having assumed that the X-containing sperm were male-producing. But in 1905 Stevens and Wilson both brought forward detailed cytological proof of the main principle—showing, however, that the X-containing sperm were female-producing, inasmuch as the female contained two X's. Thus the case for the chromosomes' constituting the basis of heredity no longer remained dependent upon the general parallelism between their mode of behavior and that of the Mendelian factors, as this line of evidence was now supplemented by the proof that given character-differences of prime importance were in fact bound up with the transmission of given chromosomes. In this way cytology became very definitely implanted into the science of heredity.

Stimulated by these findings, and being at the same time in both home and laboratory environments that were more than ever conducive to creative work, Wilson was now entering upon the years of his most productive researches—1905 to 1912. It was in this period that his series of eight classical "Studies on Chromosomes," based upon the intensive observation and analysis of a great array of exquisite preparations, mainly of Hemipteran spermatogenesis, was published. In these "Studies" and in Wilson's accessory articles of the same period we find the working out of the whole general theory of sex determination, Mendelian in principle, that forms the basis of our modern conception of this subject. Wilson's comparative observations showed that, in different species, the heterogametic sex might have the X's and Y's equal or unequal in size, that one of the other members might be dual or even multiple, and that all gradations existed from Y's equal to the X through smaller and smaller ones down to the "XO" condition. On the basis of this evidence he postulated (1906 *et seq.*) that the Y had undergone a continued degeneration, and in 1909

(Study V) he adduced more definitive genetic evidence of its being either inactive or representing "an excess of chromatin that is duplicated elsewhere in the chromosome group," in his finding of apparently normal females (as well as males) in *Metapodius* having one or more supernumerary Y's or Y-parts, and of males lacking a Y. In the same paper (1909) he explained the origin of these cases through failure of separation of the X and Y, an aberration which he had observed to occur occasionally in spermatogenesis, and he pointed out that this would in fact be a method of origination of the XO type. When, four years later, Bridges encountered the same phenomenon in breeding experiments with *Drosophila*, he and Wilson, in consultation together, agreed to term the process "non-disjunction."

By the same evidence, Wilson showed that it is the X which is the active chromosome in sex-determination, and that it differs qualitatively from the Y—"perhaps as the bearer of a specific substance (enzyme?) that calls forth a definite reaction on the part of the developing individual" (1909). Following up an earlier suggestion of Stevens (1906), he further postulated (1912) that there is still, in "X Y" forms, a part of the X more or less homologous with Y, but that the sex-determining material lies in the other part. This idea is surprisingly near the truth as we now conceive it, except for the added suggestion that the differentiating factors for sex-linked characters lie in that part of the X homologous with the Y.

Laying aside, after some consideration, the "unit-character" idea of sex proposed by Castle, according to which a given member of a chromosome pair carried "maleness" or "femaleness" *per se* and these were allelic characters for which both sexes were heterozygous (a scheme that had the additional difficulty of requiring selective fertilization), Wilson in 1909 developed further his own view that the material of the X chromosomes did not bear either maleness or femaleness in any absolute

sense but was of such a nature that, when acting in combination with the rest of the genotype, the amount present in one chromosome reacted to such a degree as to result in maleness, while that in two chromosomes, reacting more intensely, resulted in femaleness. This of course conformed just as well as Castle's scheme with the principles of Mendelian transmission—though that was realized by few Mendelians at first, and it provided just as critical an illustration of a segregating character whose distribution followed that of the chromosomes of a given pair.

The types in which the female is heterogametic in respect to sex determination were also brought into Wilson's scheme finally, but by a more roundabout route. It had been shown by Punnett and Bateson (1908) that the results of Doncaster and Raynor on what we now call sex-linkage in the moth *Abraxas*, as well as similar results in birds, were best interpreted on the basis of (1) the female being the sex-heterozygote in these cases (they did not regard it as surprising that in other large groups, on the contrary, as shown by Wilson and Stevens, the male was the sex-heterozygote), and (2) the existence of "repulsion" between the "factor for femaleness" and the dominant factor for the color character studied. They preferred not to interpret these phenomena in terms of chromosomes (partly because this would require the "dominance of an absence" in XO forms), but Spillman in the same year (1908) proposed this interpretation. Wilson, after having considered this and the somewhat similar suggestion of Castle's (1909) with reference to these types, accepted this converse sex-chromosomal scheme for these forms, on the basis of the evidence from sex-linkage. In the seventh Study (written in 1910, published in 1911) he gave diagrams of this and pointed out that the lack of XY figures in the males of all Lepidoptera and birds thus far examined was in good agreement with the conception.

A point of great theoretical interest in Spillman's de-

duction of 1908 (though one not emphasized by him) lay in the implication that there are other Mendelian characters, besides sex itself, dependent upon or linked with the chromosomes of the sex-determining pair. Wilson in his seventh Study stressed the importance of this and of the essentially similar facts which had meanwhile been discovered by Morgan in *Drosophila*, where—thanks to Stevens—the cytological picture had already been worked out. Owing to her having proved in 1908 that the *Drosophila* male was heterogametic for the sex chromosomes the mode of inheritance found by Morgan left no doubt of the truth of the inference, proposed both by Morgan and by Wilson in 1910 (see Wilson, 1914), that the dominant sex-linked genes went with the X chromosome in its segregation. Although for a time Wilson thought that this linkage might be an expression of what is now called “chromosome linkage,” he soon came to see in it a corroboration of the conception of the compoundness of the chromosomes which he espoused (see below), as well as of that of the multiple nature of the hereditary basis of characters.

The investigation of sex-determination in itself was but one aspect of Wilson's chromosome studies. He probably regarded as of greater significance the evidence they gave concerning even more basic problems, such as that of chromosome individuality, or “genetic continuity,” as he preferred to call it. This was a principle still widely contested, even by such leaders as O. Hertwig, and some destructive critics, like Fick, were contending that the chromosomes were nothing more than crystallization products formed anew in each cell-generation from the general nuclear material. In part, as Wilson and Stevens both pointed out, striking evidence of chromosome individuality could be derived, secondarily, from the facts of sex-determination themselves. For, according to the only scheme that worked, the egg with one X to begin with that received another X from the sperm came to have two X's and kept both of these throughout all its subse-

quent divisions up to the next reduction, while, *mutatis mutandis*, the egg that received a Y retained the XY combination throughout development. This would have been good enough in itself, but the facts found by Wilson went a good deal further. Thus, the considerable diversity of different individuals of the bug *Metapodius*, and of some other species, in regard to their number of chromosomes (referred to on p. 144), was combined with a constancy of the chromosome configuration throughout the unreduced cells of each individual. Hence, even in the case of unusual chromosome configurations, each of the chromosomes that had been received at fertilization (or a replica of it) reappeared after the successive resting periods during which it had seemed obliterated. Moreover, in these test cases where the configuration was aberrant, the chromosomes showed this persistency not only in their number and their individual morphology (size and form) but also in their behavior, for the extra Y's showed their peculiar reactions of remaining more condensed, undergoing late conjugation, etc. The most demonstrative case of this sort was supplied by an individual of *Metapodius* observed by Wilson in 1910, in which there chanced to be no Y, but three of the small "m-chromosomes," so that the total chromosome number was normal. Here it was evident that an *m* could not take the place of a Y, and all three *m*'s alike showed the peculiar meiotic behavior which Wilson had previously found to be characteristic of the two *m*'s of normally constituted individuals.

Going beyond the individuality of the chromosomes as wholes, Wilson adduced indirect evidence of their being compounded of parts each having their own individualities. This was largely derived from comparisons of related species, in which the X might appear as one entire chromosome or as more or less subdivided (though still of the same total mass, relative to the rest), or in which, in still other cases, a chromosome seemed to have had a portion detached that had become attached elsewhere.

Wilson concluded (seventh Study) that the exact conformation of the chromosomes as wholes was a relatively unimportant matter in the determination of characters, and that it could be changed by breakage, as well as by fusion of smaller parts in which the genetic continuity really resided. In some groups, he observed, the interspecific variability of the configurations was much greater than in other groups, and he was inclined to believe that in the latter cases wide-spread rearrangements might occur. By 1913 he was ready to assert that "microscopical investigation (independent of experiments in heredity) has made it almost certain that the chromosome is a compound body, which includes many smaller elements, . . . each of which may play a definite part in determination."

As pointing towards a possible basis for a far-reaching genetic continuity of the chromosomes, Wilson in 1909 and again in several later papers called special attention to the results obtained in 1908 *et seq.* by Bonnevie (who afterwards came to work with Wilson for a time), and later obtained by other workers. According to these, the prophase chromosomes, in rapidly dividing cells of widely different forms, could be seen each to consist of a coiled thread (later called the "chromonema"), that had been directly (or according to the earlier accounts "endogenously") derived from a similar coiled thread of a preceding telophase chromosome. In this connection, however, it should be noted that, after making careful observations of his own on the matter, Wilson continued for many years to regard this doctrine as far from established, and he still gave serious consideration to the earlier views of the proponents of chromosome individuality. According to these, the various differentiated portions of the chromosomes that are aligned in single file at mitosis become branched out (Boveri) or even to some extent diffused during the telophase and resting stages and later, during the early prophase of the next mitosis, become retracted again, if not somehow reformed, into their determinate mitotic positions.

A serious gap in the evidence for the genetic continuity of the chromosomes and their parts and for their constituting the basis of Mendelian transmission lay in the extraordinary obscurity still shrouding the cytological phenomena in many objects during the stages of synapsis and reduction, where the events most crucial for genetics would have to occur. The very existence of conjugation of homologous chromosomes was still violently contested, and even where conceded was more often considered to be an endwise pairing (telosynapsis) than a longitudinal one (parasynapsis). The latter process, which had been described more especially by Winiwarter, Strasburger, Janssens and the Schreiners, seemed to be required on the chromosome theory of heredity if the then accumulating indications of the existence of more separable hereditary factors than chromosome pairs were trustworthy. For it would give opportunity for orderly interchange of factors, as proposed by de Vries, Correns and Janssens (see below). As yet, however, these proposals seemed on the plane of speculation. Taking the mass of destructive criticism seriously, Wilson reexamined the subject "in a distinctly sceptical spirit," and made a searching and objective investigation not only of preparations of his own but also of amphibian and annelid (*Tomopteris*) material borrowed from Janssens and the Schreiners, and some Orthopteran material from McClung. In his eighth Study (1912) he emerged convinced by this examination not merely that synapsis does occur, but that, in all the material observed by him which was suitable for throwing light on the question, it occurred by longitudinal pairing.

In the amphibian and *Tomopteris* material the Y figures formed by what we should now call the "zipper action" of the partners were plainly visible, and the consequent halving of the number of visible threads was made more apparent by the fact that at this time the stems of the Y's tended to lie parallel, resulting in a "bouquet" figure. There were indications of the same process in the Orthoptera (which McClung had thought



not to have parasynapsis), but the observations here were obscured by the lesser degree of parallel orientation. In Wilson's Hemipteran material the stage of synapsis unfortunately occurred just at the moment when nearly everything in the fixed specimens was rendered indistinguishable by a contraction ("synezesis") of the chromatin contents of the nucleus, but in the stages just before and after this the conformations were seen to be essentially like those in the material in which the process of conjugation could be directly observed. The sex chromosomes in the Hemiptera afforded evidence on the question from a different angle. Remaining in a condensed condition, they could not undergo a real parasynapsis, yet they retained their identifiability throughout and could be seen to show a distinct tendency to come together. The *m* chromosomes also were aberrant, in appearing as separate chromosomes during most of the synaptic period, yet they too later, when in a condensed condition, underwent a sort of touch-and-go conjugation that could be seen very clearly. Thus these chromosomes of special types, partly because of the very lack of intimacy of the process of synapsis in them, were unusually favorable objects for demonstrating both the persistence of chromosome individuality and the reality of the pairing process in general and of the following process of segregation of the partners.

As for the ordinary chromosomes, in the stage of "pachytene" (thick threads), immediately following their conjugation, visible evidence of a persisting duality of the threads could not be obtained and so the question of the degree to which the partners might have actually fused could not be solved by direct observation. Wilson noted, however, that the impress of their dual nature was evident in their "valence," as expressed by their later forming tetrads, in contrast to the behavior of chromosomes like the X and Y in much of the Hemipteran material, and the *m*'s. For the chromosomes of these special types, which emerged from the synapsis and pachytene

stages still recognizably separate, formed only diads, at least until the time of their delayed conjugation, in condensed condition. On the basis of this comparison, it was inferred that the ordinary chromosomes, which had appeared to unite completely in synapsis, nevertheless retained within them some features of their originally dual nature.

The above evidence did not mean for Wilson, however, that the chromosomes behaved as indivisible units in synapsis. For, following Boveri, de Vries, Strasburger and Janssens, he saw in the intimacy of the parasynaptic union of the more typical chromosomes an opportunity for some sort of exchange of material, as indicated by the above-mentioned results in Mendelian heredity (which indicated that there were probably more separable genes than chromosomes). And in particular the demonstration by Morgan in 1911 of the exchange of sex-linked genes in *Drosophila*, and Morgan's novel application of Janssen's "chiasmatype" hypothesis of 1909 to explain the fact that these genes showed different degrees of linkage, were from the first regarded by Wilson as most significant. They did much to strengthen him in his conclusions, while, on the other hand, he on his side is to be credited directly and indirectly, as will appear below, with a considerable share in the development of the *Drosophila* work during the immediately following, most formative stages of its existence.

In this period Wilson's conception of the nature of the hereditary material and its relation to the characters of the organism came much closer to the modern one than did that of most Mendelians. This was largely because of his better grasp of three things: (1) the complex physiological relationships of the parts of the organism with one another (as had been brought out long before in his "General Biology"), (2) the mutual reactions of parts with one another during development, as illustrated in many of his and other workers' experiments with eggs and embryos, (3) the nature of the material basis of

heredity, as indicated by the studies on chromosomes and chromatin which now formed his chief interest. Thus he saw beyond the narrow morphological range of the unit-character geneticists and, in an address given in 1911 and again in a paper of 1912 (Study VIII), in nearly identical wording, he gave them the following much-needed admonition:

. . . Every character is produced as a reaction of the germ considered as a whole or unit-system. Characters are "borne" (if the expression is permissible at all) by this system as a whole; and the "unit-factors" . . . need be considered only as specific, differential factors of ontogenetic reaction in a complex organic system. Many "unit-characters" are known to depend upon a number of such unit-factors, in some cases probably upon a large number; and they may be definitely altered this way or that by varying the particular combinations of these factors. But any unit-factor produces its characteristic effect only in so far as it forms a part of a more general apparatus of ontogenetic reaction constituted directly or indirectly by the organism as a whole.

At other points in the same two articles Wilson entered into a discussion of the composition of the hereditary material which, like the discussion above, served as forerunner of our present view-point. We may note especially the following:

Kossel makes the pregnant remark that every peculiarity of the species and every occurrence affecting the individual may be indicated by special combinations of protein "Bausteine." The facts lead us to seek for such compounds (substances) in the chromatin or the chromosomes. It can hardly be said that even a beginning has been made in the chemical investigation of the distribution of the chromatin-substances within the nucleus. Cytologically, however, a long series of the most significant facts have been made known in respect to their groupings and modes of distribution . . . and the fact is now more than ever evident that they run parallel to the factors of determination and heredity. . . . It is difficult to see what meaning such processes [the preparations for ordinary mitosis and for the meiotic divisions] can have if they do not involve a linear alignment of different substances which are thus brought into a particular disposition for ensuing processes of division (Roux) or of paired association (Strasburger).

For Wilson, the interest in these matters lay not only in their bearing on the nature of the existing organism and its ontogeny, but also, as previously mentioned, on the related problem of the way in which it has evolved. He realized that the genetic mechanism above discussed

left little room for Darwin's "pangenesis" or other hypotheses deriving the germ plasm from the soma, and made it necessary to look for other causes of germinal variation. Finding no basis for "*entelleche's*" or other fairy tales, he nevertheless—unlike some of his contemporaries among experimental biologists—did not seek to evade the truth that the most amazing thing about life is its complexity of adaptation to self-perpetuation. In this sense, then, as he stated in 1907, Brooks's old epigram is true, that "the essence of life is not protoplasm but purpose." To increasingly explain this by natural processes, in the light of knowledge concerning the nature of the germ plasm, was in Wilson's view one of the greatest objectives of biological work.

In discussions of this problem, he repeatedly returned to consider the theory of natural selection. Thus in 1907 he said: "Evolution by natural selection resolves itself into a series of lucky accidents. . . . For natural selection, pure and simple, the fit is that which happens to fit. I, for one, am unable to find a flaw in this conception of the fit; and perhaps we may be forced to accept it as sufficient. But I believe that naturalists do not yet rest content with it." And in 1915, after recounting the shortcomings of Darwin's views, including Darwin's failure to distinguish between heritable and non-heritable variations, Wilson continued:

We should, no doubt, make a larger allowance for the role of single "lucky accidents" than did many of the earlier evolutionists. And yet, as far as the essence of the principle is concerned, I am bound to make confession of my doubts whether any existing discussion of this problem affords more food for reflection, even today, than that contained in the sixth and seventh chapters of the "*Origin of Species*" and elsewhere in the works of Darwin . . . we have made it the mode to minimize Darwin's theory . . . but . . . we should take heed how we underestimate the one really simple and intelligible explanation of organic adaptation, inadequate though it may now seem, that has thus far been placed in our hands. . . . While science viewed at close range seems always to grow more complex, a wider vision shows that her signal discoveries are often singularly simple.

In 1930, however, Wilson was "not yet quite ready to admit that higgledy-piggledy can provide an adequate ex-

planation of organic adaptations." It is probable that most geneticists to-day would go considerably farther in their incorporation of natural selection into their conception of evolution. Probably they would whole-heartedly accept the application of the fundamental principle involved to the mutational changes and recombinations of genetically continuing and multiplying chromosomes and chromosome parts, and would admit that in this form natural selection constitutes an integral part—in fact, in a sense the crux—of the explanation of the adaptiveness of all living things. But the views of Wilson on this subject, cautious though they were, were much in advance of those of the great majority of his contemporaries among the Mendelians, and, when compared with these, are clearly seen to lead in the direction of the genetic standpoint of to-day.

The excitement of the advances in chromosome theory made by Wilson in 1905–1910 communicated itself through the department of zoology at Columbia. This helps to explain why it was that most of the first batch of youngsters who became *Drosophila* workers with Morgan had been undergraduates in Columbia College in the latter part of this period and that others came through by the same route soon afterwards. Lured on by their first course in biology, where they were moulded by Sedgwick and Wilson's text and by the teaching of Calkins and McGregor, both former students of Wilson's, some of them had the privilege of taking in their sophomore year Wilson's thrilling one-semester course on heredity and the chromosomes, variation and evolution. In this the text chosen by Wilson was Lock's extraordinary book of 1906—too far "ahead of its time" to be sufficiently remembered now—which, with less caution and fewer qualifications than employed by Wilson himself, advocated the sufficiency of Mendelism, multiple factors, the chromosome theory (including exchange of linearly arranged genes during parasynapsis, after de Vries) and the natural selection of mutations, as the basis of all heredity and

evolution. Wilson's superb course on cytology, with its unequalled laboratory training and demonstrations, was usually taken by them in their third or fourth year after entering as freshmen. After this stimulating and thoroughly systematic preparation their embarkation upon the adventure of the fascinating new work on chromosomal heredity in *Drosophila* that had just been opened up by Morgan (1910 and 1911) was the logical continuation, now grown more specific in its direction, of the quest to which they had already become dedicated, calling for the ways of thinking, the knowledge and to some extent even the technique acquired during their previous years of training. And the striking similarity in the attitude of all of them towards the new problems was in no small measure a reflection of the degree to which this common training had been driven home. Thus it is likely that only these *Drosophila* workers, of the earlier years, fully realize to what an extent modern genetics traces its descent through Wilson.

Wilson was himself captivated by the *Drosophila* work—an attitude which he transmitted to his students—and he kept in close touch with it. When a discovery was made in the work he was as pleased as if it were his own. He also appeared from the first as an advocate of the work before other biologists (*e.g.*, in Studies VII and VIII), and he was active in incorporating its results into his system of concepts. Already in April, 1913, in a lecture at the University of Pennsylvania, after restating the evidence from Boveri's work on marine eggs and from his own on sex-determination—which "has definitely established the fact that the chromosomes are causal agents in heredity"—and after presenting the chromosomal interpretation of Mendelism and linkage, he went on to discuss the "attempt . . . made by Sturtevant to calculate from the observed results the degree and character of the twisting of the chromosomes and the relative position of the different specific elements within them." "This," he said, "admittedly is a bold venture

into a highly hypothetical region. Its justification is the pragmatic one that it 'works.' The hypothesis gives us the only intelligible explanation that has yet been offered . . . it is just by such venturesome advances that new possibilities of discovery are opened."

In his Croonian Lecture before the Royal Society, in 1914, he further stressed this evidence for crossing over as well as that, obtained in the meantime, of the correspondence between the numbers and sizes of the linkage groups and of the chromosomes in *Drosophila*. In summing up, he declared that "the conclusion has become irresistible that the chromosomes are the bearers of the 'factors' or 'gens.' " At the same time, elegant chromosome studies of other species of *Drosophila* were being made by Metz, working primarily as a student of Wilson's, which not only gave instructive examples of the types of variation of the chromosome configuration from species to species but, through comparison with the breeding results, obtained later, laid the way for a convincing extension of the above cytogenetic parallelism between chromosomes and linkage groups to several other species.

Wilson carefully examined the cytological evidence for crossing over then extant, but saw that it was not yet of a sufficiently critical nature. In 1920, in the course of a critique of the chiasmotype theory, he stated:

I am not able to escape the conviction that somewhere in the course of meiosis some such process must take place as is postulated by Janssens and by Morgan and his co-workers, though I must admit that this opinion rests less on cytological evidence than on genetic. . . . The truth is that for the time being genetic development of the chromosome-theory has far outrun the cytological. We are in no position to predict when the plodding progress of cytology may be able to close the gap: nevertheless we have every reason to hope that the physical mechanism of the recombination-phenomena may in the end prove to be accessible to decisive cytological demonstration.

This expectation has now in some considerable measure been realized, but only during the past decade. In the meantime, however, there were other important questions of cell theory having a bearing on genetics which called for investigation, and in the attack on which micro-



scopic observation still remained obviously the superior, if not the sole available technique. It was mainly to such questions that Wilson devoted his attention in the cytological researches of his later years.

#### ESTABLISHING THE UNIQUENESS OF THE CHROMOSOMAL ROLE

Wilson's later studies on the organization of the egg have already been mentioned. The other questions with which the researches of his later years were concerned might all be considered variants of the more general problem of to what degree other constituents of the cell than the chromatin may serve as the material basis of heredity. This problem was not one to be taken lightly, for in the case of the chloroplastids definite proof had long before been adduced not merely of their genetic continuity in a general sense but also of the property, which they share with chromosomal genes, of self-perpetuation (involving reproduction) of characteristics differentiating them amongst each other. Since this was true of chloroplastids, might it not, as some authors claimed, be true of chondriosomes, which according to one school of investigators are identical with or give rise to plastids, and might it not be true of other "formed" or "unformed" constituents of the cell?

Wilson kept this question separate from the claim that had sometimes been put forward that the cytoplasm must be as important or more important in heredity than the nucleus in the determination of the fundamental features of early development. It had been argued that this was proved by the observations that had shown the importance, for development, of the pattern of organization of the egg, and by the reciprocal hybridization experiments that had shown the predominant maternal determination of early embryonic stages. In opposition to this argument, Wilson pointed out on various occasions (*e.g.*, in "The Cell," 1925) that the organization of the egg had been proved to be "epigenetically" produced, and that

there had in consequence been every opportunity for the chromatin at a preceding stage to affect or control the egg's cytoplasmic organization. "The whole force of the evidence," said Wilson in 1925 (and he had expressed himself similarly much earlier), "drives us to the conclusion *that the chromosomes are as much concerned in the determination of the so-called 'pre-formed' or cytoplasmic characters as in any others*" (italics his). And, as he noted, there are in fact various known illustrations of such determination. Similarly, Wilson looked askance at the claim (by Loeb, Jenkinson and others) that the more ancient characteristics, differentiating the larger groups, were less likely to be chromosomal than the minor differences between individuals or races ("The Cell," 1925, p. 1015).

It is true that Wilson had stated, as early as 1906, "I no longer hold the view that the nucleus can be considered as the actual formative center of the cell," but he qualified this by adding, "it still seems to me very probable that the formative processes are directly or indirectly under its control, as has been advocated by many students of cell-physiology." At times he even went so far as to say that the chromosomes are probably not "central governing or controlling factors in the cell" and that "the chondriosomes are very likely connected with heredity" (1913). But despite these reservations he consistently recognized the at least preponderant role of the chromatin. The question then resolved itself into this: May not cytoplasmic constituents have some share in heredity, and, if so, how much and what kind of a share? As usual, he did not rest content with answers to such a question unless they were based fairly directly on a firm foundation of material evidence.

Wilson therefore undertook, in part with Pollister, to make a detailed study (1916, 1925, 1931, 1937) of the history of both the chondriosomes, the Golgi bodies and the neutral-red bodies ("vacuome") in the spermatogenesis of scorpions, a group which he had found to show espe-

cially clear and interesting figures of these structures. During the same period, his students and collaborators Bowen, Plough, Pollister and Johnson studied these cytoplasmic bodies in insects. In the scorpions a striking finding of Wilson's was that in the genus *Centrurus* (1916) and in the related *Centruroides* (1937) the chondriosome material becomes condensed before the meiotic divisions into the form of a single ring, which then undergoes "an accurate process of division in the course of which the chondriosome material is precisely divided between the daughter cells." However, in all the other genera of scorpions examined the chondriosome material existed in these stages in the form of a considerable number (*e.g.*, 24) of separate hollow spheroids, which did not divide individually but, becoming scattered irregularly about the spindle, were apportioned with only approximate equality of numbers (5 to 7) among the four daughter cells. Thus the division of the ring in the Centrurids was inferred to represent "a special case, presumably derived from a process of random segregation, as occurs in animals generally."

As for the Golgi bodies, although they underwent remarkable transformations and regroupings at different stages, they were found, even in the Centrurids, to be "distributed to the daughter cells separately, by an operation which offers every aspect of a simple bipolar segregation" of the group, *i.e.*, there was no separation of a half of each Golgi body to each daughter cell. In spermatozoon formation, moreover, although a part of these bodies came to form the acrosome, the main bulk was "cast out in the slough." The neutral-red bodies also became separated in a passive, inexact way, and they underwent complete elimination from the spermatids. Although the conclusion was unavoidable that both the chondriosomes and Golgi-bodies, at least, were real and functional constituents of the normal cell, and that they were continuing structures which somehow became increased in size and underwent fragmentation (not neces-

sarily at or near the time of cell division), so that their numbers were maintained, nevertheless the method of their distribution provided evidence against the assumption of inherent genetic differences between them. They "can have at most" concluded Wilson (1937), "only a very low type of individuality . . . the only actively and regularly dividing elements in these cells are the chromosomes and (presumably) the centrioles. This . . . may be set down to the credit of the chromosome theory of heredity."

#### RESYNTHESIS

Even before the rise of the *Drosophila* work a complete rewriting of "The Cell" had become imperative, in which the newer findings should be gathered together and organized and the older ones set forth anew from the point of view of the at last definitely crystallized chromosome theory of heredity. So great, however, was the range of time and subjects involved, and so much had observations, experiments and suggestions multiplied, that this was now a Herculean task. It is very improbable that anyone else than Wilson, even with Wilson's earlier editions to build upon, could have accomplished it. In fact, new findings seemed for a time, during the twenty years of the last rewriting, to be accumulating faster than it was possible even for Wilson to incorporate them into a unified account, unless this were to be of far more restricted nature, in relation to the extant body of research, than the earlier editions had been.

To add to these difficulties, Wilson's health, beginning about 1920, seriously deteriorated, causing him to be handicapped thereafter by crippling rheumatism and sometimes by attacks of dizziness. (In this connection it should be pointed out that this illness was in no way—as has elsewhere been asserted—an after-effect of the shipwreck which members of the Columbia department of zoology had experienced off Alaska in 1900: no one had suffered physically in this, and Wilson's health before 1920 had on the whole been good.) Wilson bore these

trials with a remarkable appearance of buoyancy, however, and from then on devoted a major portion of his time to his work on "The Cell."

At last, in 1925, when Wilson was sixty-nine, the completed volume, of over 1,200 pages, three times as large as the second edition, was given to the world. It was indeed as comprehensive as the previous treatments, even in relation to the mass of work that had been published in the meantime. In it virtually the whole of cytology, from the time of its birth more than a half a century before, stood integrated. It was realized by the members of the National Academy of Sciences that, in bestowing the Elliott Medal upon Wilson in 1928 in recognition of this great work, they were maintaining their own honor rather than adding to his. The book was given similar recognition by the Linnean Society.

The main points of Wilson's book will be evident from all that has gone before; a re-examination of its details here is manifestly impracticable. Moreover, it is relatively so recent, and has been so widely welcomed into every-day use by workers in the various fields covered, that a review at this time would be a supererogation. The fact that, during the later years of its preparation, the main concepts of cytology had for the time being reached a stage of comparative stability adds to its indispensability for the consideration of all researches done prior to its date of publication, inasmuch as they form, in themselves, a more or less self-contained system. With this work, if not before, Wilson has rightly been acknowledged to take a prominent place among the great "encyclopedists," if by this term we may denote those who not merely collect knowledge on a prodigious scale but also reinterpret and organize it, translate it into lucid language and make it really usable for investigators as well as for scholars.

It may here be pointed out that after the publication of Wilson's third edition of "The Cell" cytology took another sudden spurt forward in the development of its

underlying concepts. These did not contradict those which had gone before but in a sense went beneath them. Thus, in this most recent period, the significance of the property of paired association of the chromatin material, with its corollary, crossing over, has been shown, through Darlington's work, to go much further in the explanation of genetic phenomena than had previously been realized; at the same time, a unified theory of chromosome structure and structural change, built on the chromonema theory, has been built up. These advances represent the legitimate extension of the work set forth in Wilson's "Cell," proceeding in the same general direction; they connect directly with the framework of generalizations there expounded and do much to further substantiate as well as elucidate them.

#### WILSON'S ATTITUDES AND HIS INFLUENCE

The emergence of these newer concepts serves to illustrate one of the major theses in Wilson's general view of science. For no one, in word or deed, was a more convinced advocate than he of the doctrine that the truths of men are relative. As he said in his lecture "Biology," given in 1907: "Each forward step on the highway of discovery will bring to view a new horizon of regions still unknown." And in 1913, in "Heredity and Microscopical Research": "The explanation of any phenomenon only uncovers new phenomena behind it that still demand explanation, in endless succession; and such is the essential characteristic of scientific progress." In 1915, in "Science and Liberal Education," he expanded upon this theme as follows:

The fundamental concepts of science are in no better case than her weights and measures. They have no finality. They are but a means of advancing knowledge; they move as science moves. . . . No particular law of nature . . . will ever be more than approximate or probable, nor can we state it completely. . . . The profound significance of what we call natural laws lies in the fact that they tersely sum up our experience of the world at any given moment; and, above all, they endow us with a gift of prophecy that leads us on to new advances. Just here we are in sight of what is most vital, characteristic and hopeful in the spirit of modern science . . . this ideal [that of science] is, in a single word, *progress*.

In various articles Wilson has given us, in vivid and poetic language, his conception of the psychology of the scientist, and in this portrayal much in his own character stands revealed. Thus, in his article of 1915, above quoted from, he also said (*italics his*): "Science . . . should adjust our vision to the larger meanings in the material world. And by this I mean to say that *science should develop—and it should discipline—the constructive imagination.*" This, he maintains, "is the best gift of science to our intellectual life." Regarding the role of the imagination in science itself, he continued:

In every field the great discoverers have been seers, men of imaginative vision, carried onwards by swift intuition that runs far in advance of solid fact or rigorous logic and ranges freely to and fro in undiscovered realms beyond them. And this is a true creative process, one that is singularly like what we call the inspiration of the painter or the poet. It often thrills us in the same way. . . . At every point the material world overflows with half-revealed meanings about which science is forever weaving her imaginative fabrics; and at their best these have all the freedom, boldness and beauty of true works of art.

But Wilson was well aware that, unlike art, science cannot be satisfied with any construction that achieves only an inner harmony, no matter how appealing. For it has, alas for many a brilliant mental construction, to match its own creations against the phenomena of the outer world, and for this reason the discipline of its imagination must be the greater. "One conspicuous trait, indeed," said Wilson in the same article, "distinguishes the man of science—his incorrigible, almost automatic insistence upon verification. For no one better knows that the children of his imagination will live only in so far as they take on the living flesh and blood of reality in the appeal to nature. Not many of them survive the ordeal; yet they are the pioneers of progress, and the real conquerors of the world."

But for the scientist, said Wilson in 1909, in "Teaching and Research in the Natural Sciences," it is not even enough to

combine mental grasp, constructive imagination and natural aptitude, with an acquired mastery of his subject. . . . These will not avail if there be not



added an impulse that grows from a lively interest in the phenomena of nature and a spirit that demands to know the truth. The great theories of science possess a very high degree of fascination, her sweeping generalizations make a powerful appeal to the imagination. But they have been built up little by little through the hard and plodding study of concrete facts; it is only through such study that science moves forwards. Those who have not a first-hand acquaintance with the actual methods of research have no conception of the amount of "dead work" that it demands, of the concentrated patience that must be expended on purely technical processes, on the painstaking and conscientious accumulation of data that may long seem to give no tangible result. The investigator must prove all things, and he must have an insight and imagination trained to hold fast to that which is good. The motive power that carries him through his tasks is something akin to the artistic impulse, though it finds so different a mode of expression. It is in the best and largest sense the love of nature. It is a spontaneous interest in the world of natural phenomena that will spare no labor to find out the least as well as the greatest things and finds its best reward in the discovery of their orderly relations. Let the student ask himself in what way he feels drawn to the study of science and what will be his attitude towards his daily work. Is his imagination stirred only by the grand theories of science or the hope of making great discoveries? Science calls for something more direct and substantial than this. Her first demand is to know what things are and what they do. Her first interest is in concrete phenomena; in the physical features of the earth, in the substances of which things are made, in animals and plants; in the actions and interactions of things, in the relations of cause and effect among them. One who is conscious of such an interest, who can find satisfaction in the truth-seeking study of natural phenomena for their own sake as well as for the larger meanings that underlie them, has at least one of the best grounds on which to base the hope of success, and he will find scientific work worth while. Such an interest will broaden and deepen as he goes forwards. It gives the impulse that has led to all the great discoveries and all the great generalizations of science.

The above should be taken in connection with another passage, written in 1900, in which Wilson expounds upon his conception of the primary operations of science as follows:

No one, I trust, will understand me to advocate the indiscriminate accumulation of facts—for this is not method, but the absence of method. The essence of science is not the accumulation of knowledge, but its organization. Observation and experiment give us our materials, but it is the comparison and correlation of these materials that first build them into the fabric of science.

It should be noted that when Wilson used the word "progress" in the passages previously quoted he was concerned with actual human progress, in the fullest sense of the term, for his nature was a broad and under-



standing one and his sympathies were with his fellow men. He was not one of that group of chemically-pure scientists or art-for-art's-sake-alone artists who feel defiled at human contact or at any value their work may have in raising the lot of mankind. This was shown not only in his attitude towards men and things in general, but also in specific utterances. Thus, in 1909, after noting with approval the opportunities for scientific research that were rapidly being opened up in government service and in industry, he made the comment:

The significance of this is not lessened by the fact that many of these activities involve the application of scientific discovery to practical or commercial ends, that they graduate almost insensibly into work of a purely technical or industrial character. The boundary between "applied" and "pure" science has almost vanished. The day is past when the investigator could hold himself aloof from the applications of his science to practical affairs. He whose life is given wholly or in part to new applications of knowledge to human welfare may be as truly an investigator, and may serve mankind as well, as he who seeks only to extend the boundaries of knowledge. The aim of a Lister or a Pasteur is not less lofty than that of a Laplace or a Lyell.

As late as 1930, in commenting on the past quarter century's progress in lines of biology dealing with the nature of the finished organism, he said:

What first comes to mind is its splendid service to human life . . . man has built no temples more splendid than our medical schools, hospitals and institutions for medical research. . . . The new discoveries in heredity are steadily at work for the improvement of our cultivated plants and animals, while the agricultural schools and experiment stations, now at work in every state in the Union, may well merit a place on the same role of honor. . . . Our knowledge of the chemical basis . . . has at least threatened to invade the field of sociology. . . . It is in this direction that biology may justly be said to have some legitimate concern with those broader human activities, such as history, literature or ethics, which at first sight seem so remote from contact with our science.

As either scientist or artist, then, Wilson belongs in the class of those moderns, as well as those of remoter ages, who conceived of their work as an integral part of human life as a whole, and who, in addition to their direct engrossment and joy in the activity itself, derived inspiration from their consciousness of its relation to that life and of its ultimate effects thereon.

The various quotations given above should make clear much of the motivation back of Wilson's own achievements. It is apparent that, in the depth of his nature, the artist and the scientist were one. Thus to a considerable extent the same gifts and feelings which enabled him to be a great cytologist led him, on the other hand, to his deep appreciation of music and his remarkable facility in musical expression. His wide knowledge and understanding of chamber music and of its literature and his power of musical analysis were second only to his mastery of the field of cytology, while his ability as a cellist was such as to have led to his being rated by a famous musician as the foremost non-professional player in New York. For many years in fact he spent much of his leisure playing in a quartet that did include distinguished professionals. This afforded him an invigorating outlet for energies otherwise kept strictly confined. Whereas in his research work, as in his lectures, writings and general conduct he held his inner warmth of nature restrained and harnessed by his rigorous discipline to such an extent that it served as an underlying motive which seldom could break through completely to the surface, in his music this rich emotional drive had freer play and achieved a degree of release that science could give it only at rarer moments. Perhaps the opportunity for its exercise provided in this way enabled Wilson the better to hold his internal fire so firmly in rein when in the performance of his scientific labors.

It was not only in Wilson's love of the immediate objects which he contemplated and in his thrill at the symphonies of scientific law wherein they at last became reorganized and woven together that his artist's temperament played a vital role in his work. It was equally operative in his pronounced spirit of craftsmanship. In his music, this expressed itself in his being so accomplished a cellist, in his outdoor recreation, in his being a master sailor, and in his work it was evident in the felicitous manipulation of his superfine materials, in the beauty of

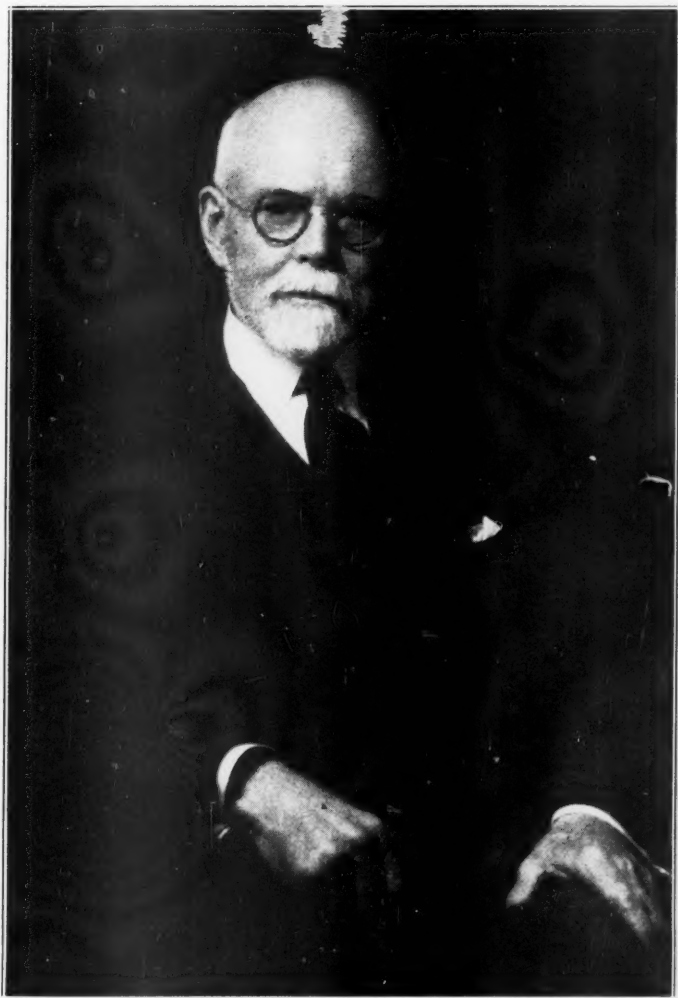
his microscope preparations and in the perfection of his drawings. No less was this spirit active in the sphere of verbal expression, in the communication of his findings and conceptions to fellow scientists, students and the public, whether through articles, books, lectures or even through ordinary conversation. Thus, each of the lectures in Wilson's various courses—introductory biology, evolution and heredity, cytology, cellular embryology and general zoology—was an artistic as well as scientific creation, a finished product of model composition; thorough in its inclusion of material, yet lucid, elegant and full of charm, and having all its parts systematically arranged and subordinated to the whole structure.

At the same time, Wilson's lectures and writings seldom displayed the literary efflorescence that his first impulse would have given them. It was his practice ruthlessly to trim them down in order the better to fit them into complete subservience to the material dealt with. This made them ideally suited to the needs of the scientist and the student, a circumstance which played an important part in the wide influence on science which Wilson came to have. The same exceptional discipline, sometimes carried to the degree of what some object to as "leaning over backward," usually dominated Wilson's criticisms of others, his rare utterances on hotly contested topics of philosophy or general affairs, his scientific theorizings, and even his outward demeanor. Thus this lover of nature and this adventurer in high places, with his soul of an artist, appeared as "a quiet gentleman."<sup>1</sup> This paradox was a fortunate one, for it was conducive to his being granted many mundane marks of recognition which, showered upon him even by those who were not in a position to appreciate his deeper meanings, helped to create conditions under which his work could prosper and could reach a wider circle of those who would really appreciate and make use of it.

<sup>1</sup> The term used in a very valuable obituary in the *New York Herald-Tribune*, March 4, 1939.

Those of his associates and students who were not so patient as Wilson himself would, however, thrill at an occasional more direct glimpse of the hidden part of his inner nature, shining through in the form—for instance—of sly humor, biting criticism or far-flung aspiration. It was refreshing, for example, to discover that in his classical paper on earthworm embryology, in 1890, he had delivered the following well-deserved rebuke to an unfair critic whom we need not name: his “paper, as a matter of course, exhibits in some degree the well-known and characteristic skill of its author in belittling the work of other investigators, but I observe with interest many signs of progress.” A similar flash was witnessed by the present writer in 1910, when, at the would-be gravest moment in a disgustingly pretentious ceremony, Wilson, sitting across the room on the platform, caught his student’s eye and risked a quiet wink. Such rare moments were the more revealing because of Wilson’s outstanding mildness, courtesy and dignity in manner, word and deed.

For Wilson’s conformity was not ordinariness, and he reserved his spirits for more worth-while ends, hidden to the passerby. Where others saw only dust or monotony, he might discern harmonies. When in his youth he had read Aristotle and Hume, it had been an expression of his ebullience, not of the desiccation that the public associates with ancient volumes. In his later years, this “quiet gentleman” was not the type of colorless professor that some who met him casually might have assumed. At sixty, Wilson could still delight in Wells’s fantasy “The First Men in the Moon,” and at 74, in his lecture of 1930 on “Biology,” he could not refrain from a sympathetic public reference to the idea of ectogenesis as depicted in Haldane’s “Daedalus.” At this age and even at 83 there still lived the Wilson who exulted in music and in the colors of Naples, who was fascinated by a beetle and an amphiastral figure, who found exhilaration alike in battling the wind and waves in his boat and



Wilson at eighty-one, in his tenth year as Professor Emeritus at Columbia, but still engaged in research. This year, 1937, marked the appearance of his last paper: that with A. W. Pollister, dealing with the method of transmission and the significance of achromatic bodies.

in helping steer the course through the restless sea of facts and hypotheses of genetics. For Wilson, in his later years, was an example of that rare type of aged persons whom it is hard for us to believe to be really old, whose minds have stayed plastic and inquiring, whose sympathies are active, and who are not increasingly engrossed in ever diminishing selves. And through it all he was of those who retain the humility of strength.

It is not surprising that he whose nature it was to love and understand the animals and even the insensate things that came within his care, and who responded so actively to the deepest feelings of great artists, should also have feelings of warmth and sympathy for the people who were under his guidance. This no less than his intellectual preeminence explains the affectionate reverence in which his students and colleagues held him, and the extent of his influence over their attitudes and concepts. His students meant very much to him, and he took his responsibilities in connection with them very seriously. By a natural reciprocation, he filled a large place in their own lives. And after they had passed out of his hands, they found that even more important to them as scientists than the facts he had taught them were the attitudes which he had helped to imbue—especially the spirit of objectivity, of criticism, of seeking out truth even in error, the demand for verification, the striving for organization, the ideal of progress.

The harmoniousness of his human relationships, and their deep meaning to him, are likewise evident in his sincere and intimate friendships, both with comrades in this country and with those whom he had met abroad, among the latter especially Anton Dohrn and Theodor Boveri. These friendships were marked by that ideal intimacy of communion throughout varied spheres of living whereby the lives of both participants experience a thoroughgoing mutual enhancement. But most brightly of all Wilson's nature shone in the profound happiness of his married life. He was married to Anne Maynard Kidder in

1903, shortly before the most creative period of his scientific work. His life with his wife, and with their daughter, Nancy—now Mrs. John Lobb,—was an idyl such as is seldom met with.

We shall not speak in detail here of the various administrative posts which Wilson filled with distinction. In all these he strove to foster that spirit of science in which he had his being. Sometimes, however, he doubted whether, with the multiplication of administrative and teaching activities in a modern university, it “could maintain an atmosphere in which scientific research and scholarship can freely breathe,” and he warned that “the leadership of the universities in intellectual progress will depend on the reply” made to that question.

Neither shall we recount here the numerous signal honors which Wilson received. They are to be found listed in various directories. They serve as indications of the breadth and the strength of the influence he exerted, though to assess the value of that influence one must know the history of cellular biology and genetics.

It is indeed fortunate, not merely for Americans but for all mankind, that Wilson should have succeeded in transferring such a vigorous scion of the cell-science of Germany and the Low Countries to this section of the English-speaking community in those years, near the turn of the century, when its growth over there was most flourishing. Equally important is the later impetus he gave it, which played so direct and crucial a part in the incorporation of cytology into genetics as its physical basis, and of which all modern work on the chromosome theory of heredity is so largely an outgrowth. In the other main section of the English-speaking community also, as well as in the U.S.S.R., Scandinavia, Japan and elsewhere, this work has for some time past been taken over, largely as a result of the success which the point of view fostered by Wilson had in this country to begin with. In consequence the work has been carried much further forward, especially in the decade now closing, in an ever greater and more coordinated world effort.



The fumes of war, spreading out from the heart of the region where the cell theory had its first rise, are now grievously choking this growth in an ever wider circle. But science must grow or retrogress. Thus the duty now falls back with increasing urgency upon us who remain, of continuing to nurture this precious and sensitive growth in our own midst, and of assisting it as best we can wherever else it may still have a chance to survive. This surely is what Wilson would have counselled. It represents the continuance to-day of the work in which he lived. And in this work and in its further extensions in times to come, so long as science lasts, his spirit will lead us forward.

## REVIEWS AND COMMENTS

EDITED BY CARL L. HUBBS

IN this section reviews and notices are given of current publications on general biology and of specialized works which have an important bearing in this general field. Emphasis is given to books and major articles which fall within the special scope of *THE AMERICAN NATURALIST*, in that they deal with the factors of organic evolution.

REVIEWS AND COMMENTS are meant to include also such general discussions, reports, news items and announcements as may be of wide interest to students of evolution. Except as otherwise indicated, all items are prepared by the Section Editor, Dr. Carl L. Hubbs, University of Michigan, Ann Arbor, Michigan. All opinions are those of the reviewer.

**Systematics and the Origin of Species.** From the Viewpoint of a Zoologist. By ERNST MAYR. New York: Columbia University Press, 1942: i-xiv, 1-334, figs. 1-29. \$4.00.

THE emergent science of speciation is notably furthered by the publication of this book—the most comprehensive treatment of the subject in the English language. The new systematics is advanced not only as a special field of inquiry but also as an integrated element in general biology. A broad groundwork of sound generalization is laid for the construction of a modern philosophy of speciation.

Of the many contributions in this volume perhaps the most helpful to American students of speciation will be the data and interpretations of European systematists—of specialists not only in birds but also in many other groups, particularly insects. Mayr's familiarity with the far-flung systematic literature is amazing.

The treatment is perhaps least adequate for the aquatic vertebrates. The great richness of data derived from racial investigations in fishes is little exploited. The "ecological rules" of the mammalogist and the ornithologist are discussed at some length, but those of the ichthyologist are inadequately presented. Little credence is given to the very strong evidence that speciation of fishes has been explosive where, as in newly formed lakes, an unsaturated set of habitats has suddenly been provided.

It is only natural that the author should stress the data and the viewpoint of systematic ornithology, and in some

ways his book has thereby been strengthened. Certain aspects of speciation can be most advantageously developed from an ornithological approach. As the reader is reminded (almost too often), birds as a class are the most completely described and named, the most extensively studied, of any group of animals. For this reason ornithology provides in general the most ample material on which to base tabular analyses of different types of speciation. Following Rensch's lead Mayr is able to summarize relatively complete arrays of case data, to contrast the insular and the continental types of differentiation; to postulate relations between dispersal and subspeciation, as on archipelagos; to determine how, where and to what degree geographic forms intergrade; and to illustrate other speciation trends. Mayr's own studies along these lines, on the birds of the now battle-torn southwestern Pacific, prove to be particularly illuminating.

In other ways, however, the treatise seems to have been weakened by the ornithocentric approach. Phenomena, interpretations and methods of study that are better illustrated by groups other than birds receive relatively little emphasis. At times the impression is given that the author is forcing the evidence derived from other groups into the pattern of speciational interpretations which he has built up from the bird data. Thus the evidence for ecological, temporal and behavioral isolation is (in my opinion) too strongly discounted, in favor of the view that almost all speciation, in other groups as well as in birds, is attributable to geographical isolation. Geographical representation as a practical species criterion (though admittedly a very important one) seems to have been overdone. There is perhaps an overstress too on the contrast between sympatric and allopatric speciation. Incidentally the etymologically hybrid terms sympatric (not isolated) and allopatric (isolated), referring to kinds as well as to speciational types, might better be written "compatric" and "alipatric."

The slight attention paid by Mayr to experimental researches (perhaps because such studies have received little emphasis in systematic ornithology) constitutes a measure of backsliding in a forward-stepping movement. Experimental work, when occasionally and briefly referred to, is relegated to genetics—as though experiment were the prerogative or characteristic of certain branches of biology, rather than a method of research available in all divisions of science. The increased application of the experimental method in systematics is surely one of the reasons why systematics and other branches of zoology are coming to a rapprochement, which in other ways Mayr has done very much to further.

The statistical approach to speciation problems though favored in principle is likewise slighted (perhaps because exact quantitative methods of analysis have been less used in ornithology than in some other branches of systematic zoology).

The line of thought that is most persistently put forth in "Systematics and the Origin of Species" is that the "morphological species concept" must be replaced by a "biological species concept." The two concepts are subjected by Mayr to a rather intense verbal contrast: the morphological criterion is held to be antiquated, unnatural, nonfunctional, static, and quite inadequate as a basis for the study of speciation; the biological species concept is said to be modern, natural, functional, dynamic, and brimful of significance for the analysis of evolution.

In only one practical application, however, is any clear difference between the concepts demonstrated. In accrediting specific rather than subspecific status, Mayr relies not on the morphological criterion of amount or kind of difference but rather on the attainment of actual or potential genetic isolation, in nature. The distinction between the ideas does not apply to pairs of forms which come into contact with one another, for on either concept the kinds are then regarded as conspecific if they interbreed and intergrade. It appears that the distinction

applies only to pairs of forms which do not come into contact: the "morphological" systematist then grants specific status if the two kinds are consistently separable, or widely different, whereas the "biological" systematist (of the Mayr school) accords the specific rank when from varied data he infers—ordinarily by necessity guesses—that the isolated forms would not freely interbreed in nature if they were to occur together. But such judgment will ordinarily have to rest on morphological evidence (as Mayr admits): if the differences between the two isolated kinds is of the order of the distinctions between forms which come together but fail to intergrade, then, by analogy, the isolated forms are called species. Yet such morphological criteria are held in disrepute, and regarded as virtually useless because many true subspecies are more distinct in characters than some full species!

Mayr's "biological species concept" ordinarily slams the door on any objective test of the specific distinctness of geographically isolated forms (for which alone it is distinctively applicable). Since his one criterion is that of genetic isolation *in nature*, one can not on his basis test the specific status of any given pair of forms by *experimental* matings. Only by transference experiments, which would very seldom be practicable to conduct or to follow critically, could one determine whether two forms would freely interbreed to produce fertile offspring in nature. This "biological species concept" would therefore force systematic procedure (and speciation considerations based thereon) into the realm of impression and authority. It seems to me that this is not the thing to do, since an outstanding need in systematics is the replacement of an impressionistic and authoritative treatment by an objective one, capable of being verified by research rather than by an agreement in opinion. It is perhaps of some significance, in this connection, that impression and authority have played a particularly strong role in bird systematics.

To define the species as Mayr does solely on the basis of actual or potential genetic isolation in nature, and to base a systematic procedure and a speciational philosophy on this sole criterion, certainly has the pedagogic advantage of simplicity—but is not thereby necessarily justified. On the contrary, the excessive complexity and variety of the speciational process renders such a definition (and theory and practice) inadequate.

The most obvious criterion of the species would seem to be the attainment of complete differentiation. Genetic isolation (actual but not potential, I would say) is one of the main criteria involved in measuring such divergence, but the evidence for genetic isolation often breaks down. As Mayr notes, a mere mutant may be more or less sterile with its parental type, whereas some distinct genera produce fertile offspring, and all grades of inter-fertility and intersterility may be observed in experimental systematics. Genetic isolation is a usual but not an invariable mark of the specific level. The same can be said of a notable amount of structural difference, or of a great complexity of differential characteristics, or of intersterility in experimental matings as well as in nature, or of sharp differences between types in behavior. I think that all such criteria need be considered, in both theory and practice.

If we accept completeness of differentiation as the test of the attainment of the species level of differentiation, and if we base our interpretations on functional as well as structural characteristics, and regard the species (and its subdivisions) as populations maintaining themselves by their own life ways in their own environments, we arrive at a species concept that is quite as modern, natural, functional and dynamic as is the "biological species concept" of the book under review.

Mayr duly emphasizes the idea that the systematic categories (minor races, subspecies, species, genera and higher groups) are populations, and his discussions are replete with indications that these populations are

marked by integrity in time and in space. He does not, however, join with other new systematists in definitely expressing the corollary that the history, consolidation and survival of a population, in other words, its successful mass reaction in the struggle for existence, constitute a systematic criterion that is quite as significant as the genetic potential. As though either ignoring or discarding this concept, Mayr writes of the instantaneous origin of new species through such means as polyploidy—rather than writing of the origin by such methods of the genetic material out of which in time new species might arise, through a long ordeal of survival and integration.

#### NOTICES OF NEW BOOKS

**The Handling of Chromosomes.** By C. D. DARLINGTON AND L. F. LA COUR. New York: The Macmillan Co., 1942: 1-162, pls. 1-16, figs. 1-7. \$2.50.—We have here an excellent *vade mecum* for the preparation of cytological material, clearly and authoritatively written. The methods must be good, if they will yield even occasionally results to compare with those shown in the 16 plates of magnificently reproduced photomicrographs.

**Man and the Biological World.** J. SPEED ROGERS, THEODORE H. HUBBELL AND C. FRANCIS BYERS. New York. McGraw-Hill Book Co., 1942: i-x, 1-607, figs. 1-180. \$3.50.—Textbooks are not often given attention in this review section, but occasionally one appears that is too outstanding to be left unnoticed. The text of the University of Florida biologists, which has now been made generally available, fits into this category. It presents with even balance the whole array of fundamental biological principles. The human aspect is stressed, but without undue emphasis. The frank viewpoint on such problems as evolution and sex is especially commendable. "Man and the Biological World" is not only an excellent text for a year's course in biology; it will also serve well as an elementary biological reference work in schools and home libraries.

**Guide to the Literature of the Zoological Sciences.** By ROGER C. SMITH. Minneapolis: Burgess Publishing Co., 1942:



i-vii, 1-128 (offset printing). \$2.00.—Students often go through their training in zoology without learning how to find and use the vast literature in this field. Only a few zoology departments offer a course (or seminar) on zoological literature. One of the best of these courses, to judge from the excellent outline in Smith's *Guide*, must be the one given at Kansas State College. "Everything a Young Student Should Know about Zoological Literature" might have been chosen as the title of this book. It tells one about the use of a library, location of titles, dictionaries, encyclopedias, gazetteers, atlases, maps, biographical dictionaries, abstract journals, preparation of bibliographies and of scientific papers, nomenclators, special indexes and species catalogs, general taxonomic works, and many other items.

**Introduction to Parasitology.** By A. S. PEARSE. Springfield and Baltimore: Charles C. Thomas, 1942: i-viii, 1-357, figs. 1-448. \$3.75.—Few biologists of the day can match Pearse in command of information or in power of synthesis. These traits are exhibited in all his books, and stand out sharply in this treatise on general parasitology. Most texts in the field are largely limited to medical parasitology, or deal almost entirely with the main groups of parasites; this one covers parasites in a broad and inclusive way. Many biologists, even some parasitologists, will be surprised to note how widely the phenomenon of parasitism is spread throughout the animal kingdom. Beyond the 8-page introduction, the treatment is entirely systematic, but much information on the life-cycles of parasites and on their ecological and pathological relations is given throughout the book. The well and interestingly written text is fortified by an abundance of fine illustrations.

**The Plant Communities of the Welaka Area.** With Special Reference to Correlations between Soils and Vegetational Succession. By ALBERT MIDDLETON LAESSLE. University of Florida Publication, Biol. Sci. Ser., 4, 1942: 1-143, pls. 1-14, figs. 1-25, maps 1-3, charts 1-2. \$1.50 plus postage.—This is a thorough ecological study of the University of Florida Conservation Reserve. It is an important contribution to plant ecology, and will serve as the basis for other researches being conducted in this area by the active biological staff of the University of Florida.

**Science in Progress.** Third Series. Edited by GEORGE A. BAITSELL. New Haven, Conn.: Yale University Press, 1942: i-xiv, 1-322, figs. 1-112. \$3.00.—The third series of the national lectureships of the Society of the Sigma Xi comprises ten lectures which were presented in 1941 and 1942 by highly competent authorities. Astronomy, physics and engineering are emphasized. Photosynthesis, one of the most complicated and fundamental of the problems of life, is presented very skilfully and interestingly for the general scientific reader by JAMES FRANCK. Medical science and physiology are represented by a chapter on a timely and important subject, "The Mode of Action of Sulfanilamide," prepared by PERRIN H. LONG. Many biologists will turn with keenest interest to V. K. ZWORYKIN's very informative article on "Image Formation of Electrons." The electron micrographs of microorganisms and of a filterable virus are very impressive. The volume maintains the high book-making standards of the Yale University Press.

**Handbook of Frogs and Toads.** By ANNA ALLEN WRIGHT AND ALBERT HAZEN WRIGHT. Ithaca, N. Y.: Comstock Publishing Co., Handbook of American Natural History, 1 [Ed. 2], 1942: i-xi, 1-286, pls. 1-88, 30 figs. \$3.00.—Bountifully illustrated and enthusiastically written, this book has been prepared for and by naturalists. It should be useful too for the many experimental biologists who employ amphibians in their researches. Systematists will criticize the lack of consistency in the nomenclature of typical subspecies: some are designated by the species binomial, thus usurping the name that properly belongs to the whole species complex; others are correctly accorded the tautonymic trinomial.

## SHORTER ARTICLES AND DISCUSSION

### INDEPENDENT IDENTICAL MUTATIONS TO ALBINISM IN THE SEX CHROMOSOME OF THE FOWL<sup>1</sup>

FOLLOWING our earlier report of a type of sex-linked, imperfect albinism in the domestic fowl, two other cases of albinism, geographically widely separated, were brought to our attention. Representatives of each were secured for study and appropriate genetic tests have now proven that these mutations are identical with that first studied by us. Because there is good evidence that the three mutations to albinism occurred quite independently, they are of sufficient interest to warrant this brief report. The histories of the three cases follow.

(1) *In New York State: in Barred Plymouth Rocks.* An albinotic chick obtained in 1939 from an Ithaca hatchery developed into a female that showed faint "ghost-barring" in the plumage and the presence of some melanin in the eye. The pupil appeared dull red. In albinotic descendants of this bird, melanin was present in small amounts in the pigment epithelium of the retina, and in the retinal portions of the ciliary body and of the iris. There was none in the choroid, which is pigmented in normal fowls. A more detailed description has been given by Mueller and Hutt (1941). Their genetic studies showed that the condition was caused by a sex-linked, recessive gene which was designated *al*.

In about 8,000 Barred Rock chicks from the flock that yielded this mutation, only the one albinotic chick was found. Any others would have been equally conspicuous and therefore none could have been overlooked. Since (1) any sire heterozygous for the mutation would have carried it in half his germ cells and caused albinism in half his daughters, (2) the average number of chicks per sire in this flock was about 270 and (3) only a single albinotic chick was obtained, it was considered probable that the sire of our first albino had not been heterozygous, but that the mutation had occurred so recently in his germ cells that only a small proportion of his spermatozoa carried the gene, *al*.

(2) *In Massachusetts: in Barred Plymouth Rocks.* Through the kindness of Dr. J. C. Scholes, of the Beacon Milling Company, Cayuga, N. Y., we obtained in 1941 an albinotic Barred

<sup>1</sup> No. 17 in the series, "Genetics of the Fowl," by the senior author.

Rock chicken that had been brought to the agency of that company in Fall River, Massachusetts. Nothing was known of its history, and apparently only one such chick was found in that locality. It seems improbable that this bird could have been related to the albinotic chick obtained at Ithaca, even though both occurred in Barred Rocks. It developed into a female that showed the same ghost-barring as did our first albino. After it matured, it was mated with an albinotic male that was homozygous for the Ithaca mutation. The results (Table 1) showed clearly that the two mutations were identical, for all the progeny were albinos. If the two mutations had been different, a ratio of 2 normal ♂♂: 1 normal ♀: 1 albinotic ♀ was to be expected.

(3) *In Indiana: in S. C. White Leghorns.* Upon following up reports of pink-eyed chicks among White Leghorns at a hatchery in La Porte, Indiana, it was learned from the proprietor that he had hatched upwards of 80 such chicks in 1941, and that all were females. This indication that a sex-linked mutation was responsible was confirmed by breeding tests at Ithaca with two albinotic Leghorns that survived to maturity from the five that were kindly sent to us as chicks by the owner of the hatchery. When these were mated at different times with two males of the Ithaca stock, one homozygous and the other heterozygous for the gene, *al*, the results were as shown in Table 1.

TABLE 1  
TESTS FOR IDENTITY OF THE MUTATIONS FROM THREE STATES

Mating	Progeny				
	Albinos			Normal	
	Males	Females	Not sexed	Males	Females
1. Ithaca ♂, H4998, <i>al al</i> , × Mass. albinotic ♀	5	5	5	0	0
2. Ithaca ♂, H4998, <i>al al</i> , × Indiana albinotic ♀ ♀	5	6	13	0	0
3. Ithaca ♂, H10042, <i>Al al</i> , × Indiana albinotic ♀ ♀	7	7		7	11

It is clear, from the data given in Table 1, that the mutation in the Indiana White Leghorns was identical with that in the Barred Rocks at Ithaca. Had it been otherwise, the second mating listed in the table would have yielded only normal males and albinotic females, and the third would have yielded a ratio of 2 normal ♂♂: 1 normal ♀: 1 albinotic ♀. The albinotic males hatched from all three matings could not have been obtained un-

less their albinotic dam carried the same gene, *al*, as did their sires. It follows that all three mutations were identical.

#### DISCUSSION

For reasons given above, it was considered that the mutation at Ithaca was discovered in the first generation after that in which it occurred. Attempts to trace the Indiana mutation further back failed. The owner of the flock to which the hatchery operator assigned the albinos stated that his White Leghorns were under official supervision in a Record of Performance program, and that any peculiarity such as albinism would certainly have been noticed, either by him or by the inspectors. Because sex-linked mutations in the fowl are bound to appear in the daughters (which are heterogametic) of any heterozygous sire, they are recognizable, if their effects are visible, soon after the mutation occurs. Unlike autosomal mutations, they are not carried along unseen for several generations until chance brings two heterozygous breeders together. It seems probable, therefore, that all three of these mutations occurred within about a year (one generation) of the time when they were discovered. This supports the other evidence that all three mutations occurred independently.

Apart from the fact that the Indiana mutation appeared about 700 miles from that found at Ithaca, the occurrence of these two in two different breeds is evidence that they arose independently, especially because both came from pure-bred flocks used to supply first-class hatcheries.

Only one case of albinism (Warren, 1933) and one of pink-eyed dilution (Warren, 1940) were reported in the fowl, so far as the writers can ascertain, in the first forty years of this century. It is somewhat of a coincidence, therefore, that there should be discovered three separate cases of albinism attributable to independent, but identical, mutations in one locus of the sex chromosome. The coincidence was heightened by the appearance in 1940 of a type of sex-linked albinism in the turkey that differs somewhat from that in the fowl (Hutt and Mueller, 1942). However, it seems probable that the appearance of these four sex-linked mutations in three years must be attributed, not to the action of any cosmic agency that might have accelerated the mutation rate, but merely to the fact that there are now more persons in the field than in earlier days who are able to recognize

items of genetic interest and who know where to send such items for study.

## SUMMARY

By breeding tests of albinotic fowls found in New York State, in Massachusetts, and in Indiana, it was shown that all three were genetically identical, and were caused by a mutation in the sex chromosome. In one case, the mutation occurred in White Leghorns; the others were in Barred Plymouth Rocks. Reasons are given for assuming that the three mutations, though genetically identical, arose quite independently.

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## EFFECTS OF SINGLE GENES ON THE BEHAVIOR OF DROSOPHILA

A NUMBER of years ago the author became interested in the problem of the practical importance of hereditary variation. What animals (or people) do is presumably more important than their appearance, which has long been known to be largely controlled by genetic factors. Therefore, an attempt was made to find a simple but important behavior trait in an animal already genetically analyzed.

It was assumed that the behavior of insects would follow a simple, unvarying pattern, and the photic response of *Drosophila melanogaster* seemed to present ideal raw material. This reaction, which Carpenter (1905) defined as the fly's tendency to move toward light when mechanically jarred, appears to be highly useful in facilitating its escape from garbage pails and cavities in rotten fruit.

Following suggestions by Dr. H. H. Strandkov, certain *Drosophila* stocks carried at the University of Chicago were investigated. Preliminary work (Scott, 1937) showed that there were distinct differences between brown and white stocks in both mean and standard deviation of the times for crawling toward a light (brown  $14.49 \pm .23$ ,  $1.46 \pm .17$  seconds; white  $21.23 \pm .76$ ,  $4.18 \pm .54$  seconds).

As these stocks had been maintained for some years by transferring a few flies to a new bottle, it was assumed that they were inbred and that the differences were genetic. It was also shown that the differences were mainly caused by an unusual sensitivity to jarring in the brown stock.

This supported the theory that important differences in behavior can be produced by heredity but gave no evidence as to the role of single genes. The next step was to test for possible effects of the two known genes in the stocks.

#### METHODS

The difficulty in this sort of experiment is to eliminate the possibility that other factors closely linked to the known genes will affect the character. In this case it was attempted to get rid of these extraneous factors by backcrossing. A red-eyed fly was crossed with one from the brown stock and a red-eyed daughter (in which crossing-over could occur) was backcrossed to the brown stock. Her red-eyed daughter was again backcrossed and this was repeated so that in each generation there was an opportunity for some of the extraneous genes brought in by the original red-eyed fly to be lost. The same procedure was used in the white stock.

The reaction of the flies to light was tested by essentially the same method which was used in previous work (Scott, 1937), except that it was possible to keep environmental conditions much more closely controlled. Normal and mutant flies could be raised in the same bottle from the same parent and be tested within a period of two hours.

The apparatus used is shown in Fig. 1, and the primary data obtained with it represent the median times for a group of 19 flies to start and crawl a horizontal distance slightly greater than 18.3 cm, in a beam of light ranging in power from 6-16 foot candles, at a temperature of 24-25° C., and under conditions in which the only vibration came from the flies running into each



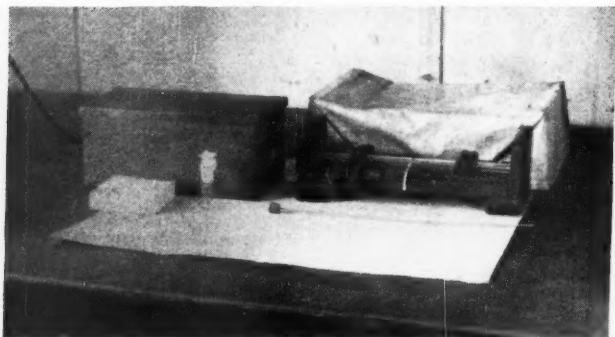


FIG. 1. Apparatus for measuring the reaction of *Drosophila* to light. On the right, a rack holding a glass tube with removable end sections, an opaque cover, and a cork plunger for pushing the flies down into one end of the tube. On the left, a box holding an electric light, and an isolation vial and box in which flies are kept previous to testing.

other, the handling of the tube and the raising of the barrier. In comparisons, the mean and variance of ten consecutive trials in one group were matched against similar results taken immediately afterward from the other group.

#### DATA

TABLE 1

NORMAL ALLELOMORPH OF *bw* BACKCROSSED INTO BROWN STOCK. FIRST SERIES, 12-13 CROSS-OVER GENERATIONS. TIME IN SECONDS

Brown <i>bw/bw</i>				Red <i>bw/+</i>			
n	Mean	Variance	SD	n	Mean	Variance	SD
10	15.27	2.54		10	17.32	4.17	
10	11.29	.93		10	11.14	2.41	
10	9.58	.39		10	12.55	3.05	
10	12.28	.77		10	10.14	1.74	
40	12.11	5.31	2.30	40	12.78	10.49	3.24
$M_{red} - M_{brown} = .67 \pm .64$				$SD_{red} - SD_{brown} = .94 \pm .44$			

The first comparison between homozygous (brown) and heterozygous (red) flies in the brown stock (Table 1) showed a small but significant difference in variability as measured by the standard deviation. There was also a difference in the mean, but not large enough to be significant. The backcrossed flies were lost before a long series of experiments could be done, and the normal allelomorph was again crossed into the brown stock.

TABLE 2

NORMAL ALLELOMORPH OF *bw* BACKCROSSED INTO BROWN STOCK. SECOND SERIES, 13-17 CROSS-OVER GENERATIONS

Brown <i>bw/bw</i>				Red <i>bw/+</i>			
n	Mean	Variance	SD	n	Mean	Variance	SD
9	10.90	.63		10	11.53	.27	
10	9.50	.64		10	9.90	1.03	
10	12.50	1.17		9	11.51	.97	
10	10.42	.24		9	10.97	2.61	
10	10.05	1.03		10	10.96	1.14	
10	12.72	.99		10	13.36	2.12	
9	13.77	2.31		8	12.28	1.62	
68	11.40	3.04	1.74	66	11.48	2.58	1.61
$M_{red} - M_{brown} = .08 \pm .29$				$SD_{brown} - SD_{red} = .13 \pm .21$			

In this second experiment there was no significant difference between the two types of flies. It can be concluded that in this stock the brown eye color probably had no important effect on the reaction to light and vibration.

TABLE 3

NORMAL ALLELOMORPH OF *w* BACKCROSSED INTO WHITE STOCK, 19-24 CROSS-OVER GENERATIONS

White <i>w/</i>				Red <i>+/</i>			
n	Mean	Variance	SD	n	Mean	Variance	SD
9	19.30	9.70		9	30.30	175.97	
10	21.08	17.34		10	34.04	483.08	
9	22.37	37.81		9	29.74	245.27	
9	22.86	87.44		9	39.88	533.81	
10	20.46	10.39		9	25.97	72.77	
47	21.19	35.55	5.79	46	32.03	327.89	18.10
$M_{red} - M_{white} = 10.84 \pm 2.84$				$SD_{red} - SD_{white} = 12.31 \pm 1.98$			

In the meantime a similar experiment had been done within the white stock. After a large number of opportunities for crossing-over, important differences in the mean and standard deviation for white and red-eyed flies were found, and these effects may be attributed to the section of the chromosome which remained attached to the *w* gene, and probably to that gene itself.

In short, the brown and white-eyed stocks showed very great differences in behavior under comparable conditions. The brown-eyed flies were about ten seconds faster than the white on the average, and showed very much less variability. As a working hypothesis it might be supposed that the differences were caused by the brown and white eye colors or some other effects of the *bw* (brown) and *w* (white) genes. If this were true it would be expected that removing these genes would make the two stocks alike. No such result was obtained. Red-eyed flies of the brown

stock were almost exactly the same as the browns, and red-eyed flies of the white stock were even slower than the whites.

#### DISCUSSION

These results seem to indicate that an important effect on behavior can be produced by a single gene. However, as Schwab (1940) and others have pointed out, it is almost impossible to be sure that modifying factors on the same chromosome have not been carried along with the white gene. Even with twenty generations of backcrossing there is a good chance that no loss of genes has taken place within a chromosome distance corresponding to a five per cent. cross-over value.

On the other hand, there are good reasons for supposing that the white gene is itself responsible for the effect. Located within one and a half units of the end of the chromosome, a large number of linked genes could be carried only on one side of it. Furthermore, there is a ready explanation for the effect on behavior. According to McEwen (1917), the pigment in the eye of *Drosophila* is so placed as to cut out some of the light which enters each facet. A colorless eye should transmit more light than a red one, and since the speed of walking toward a light is proportional to intensity (Cole, 1922), a white-eyed fly should be faster than a red-eyed one. Even without these considerations, it can be said that a relatively short piece of the first chromosome adjacent to white can produce an important effect on behavior.

In fact, this segment of the chromosome may make the difference between flies giving a reaction to light and remaining inactive, as in many cases the red-eyed flies did not crawl at all. The conditions under which the experiment was done (a minimum amount of vibration and a weak light) appear to have been very close to a threshold point for this stock, below which the flies would not react. If so, a small genetic lowering of the reaction time in the red-eyed flies would account for the great lowering of the average time and large increase in the amount of variability observed. It thus appears that the importance of the effect was partly dependent on the presence of a threshold. Such a condition would, of course, magnify any differences, genetic or environmental.

It is obvious that more than one genetic factor can modify the behavior of *Drosophila*. The original red-eyed flies which were crossed into the white stock were faster than the white (Mean

$17.89 \pm 0.59$ , SD  $3.25 \pm 0.42$ ), but after repeated back-crossing were slower than the white. This sort of result has been described by Dobzhansky (1927) and Schwab (1940) in studies on spermatheca shape, and it may be explained by the presence of another factor or factors which also speeded up the reaction and which were eliminated by back-crossing. And there must have been still another factor or factors which would account for the difference between the brown and white stocks.

The data are limited by the difficulties and laboriousness of the method. Nevertheless, a general picture of the causes of variability in the photic reaction in *Drosophila* can be painted with some degree of certainty. There are probably several independent genetic factors, some tending to increase the speed of reaction and some to decrease it. There are also several variable environmental factors, such as light, vibration, temperature and conditions of nutrition. The importance of the effects of these various causes may be magnified near a threshold. If both were uncontrolled, an extraordinary multiplicity of effects would be expected. This is very different from the interpretation of insect behavior which was given by early naturalists such as Fabre.

Even when the same group of flies was tested and hereditary differences could not affect the data, and when every effort was made to keep environmental conditions the same, a great deal of variability was observed. This can be seen in the tables. If hereditary variability (which is probably more important in laboratory raised flies) is added to this, it can only be concluded that *Drosophila* is capable of a great deal of individual variation and adjustment in its behavior.

As to the original problem of the importance of hereditary variation, a large effect on behavior can be produced by a relatively small piece of a chromosome and probably by a single gene. This indicates a general possibility which can only be disregarded when uniform heredity is secured by inbreeding or other means.

It has been shown that the large effect of the white gene was probably dependent on a set of environmental conditions involving a threshold. On the other hand, the effects of minor environmental changes are dependent on heredity, since they produced a large amount of variability in series of tests on the same red-eyed flies and a much smaller amount in corresponding tests on the whites. With this interdependence of heredity and environ-

ment it is impossible to give any general rule as to their relative effects. It is enough to say that heredity *can* be important, and that genetic factors are apt to increase in relative importance as environmental conditions are made constant.

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THE RATE OF ROOT ELONGATION IN DIPLOID AND  
TETRAPLOID SUDAN GRASS AND RYE

It is common knowledge that the artificially produced tetraploids in grasses, at least, are slower growing than the diploids from which they are derived. In fact, it is almost the rule. However, no information is available for the rate of elongation, *i.e.*, growth, of roots from germinating seeds for a comparison of diploid and tetraploid lines of the same species.

Seed of tetraploid Sudan grass was obtained from Dr. R. J. Garber, of the U. S. Regional Pasture Research Laboratory, State College, Pennsylvania, and seed of tetraploid rye was obtained from Dr. E. Dorsey, Cornell University. The Division of Entomology of the University of Minnesota cooperated by making available controlled temperature chambers. Only the diploid rye is of the same variety as the tetraploid.

All seeds were soaked for an hour and germinated on moist filter paper at a number of different temperatures. Measurements were taken in millimeters every 12 hours for three days. The results of this experiment are found in Tables 1 and 2.

At all temperatures, excepting 40° C., the roots of tetraploid Sudan grass elongated at a faster rate than the diploid Sudan grass. The diploid rye roots grew faster than the tetraploid rye at all temperatures. These differences were also reflected in the

TABLE 1  
 SUDAN GRASS (*Sorghum sudanense*). TOTAL PERIODIC GROWTH AND PERIODIC  
 INCREMENT IN MILLIMETERS PER 12-HOUR PERIOD

		Total Periodic Growth					
		1	2	3	4	5	6
20° C.	2n	—	.2	.3	1.5	4.3	6.8
	4n	—	.8	1.5	4.6	9.6	14.7
25° C.	2n	.2	1.5	6.8	14.8	24.0	34.0
	4n	.6	3.1	11.9	24.5	36.7	50.0
30° C.	2n	.5	8.3	22.0	32.4	38.8	45.3
	4n	.9	14.9	38.7	53.3	63.5	74.1
35° C.	2n	1.1	12.2	25.2	34.0	40.5	45.9
	4n	2.2	21.3	46.9	60.8	71.0	83.4
40° C.	2n	.6	2.9	9.0	14.6	22.7	25.8
	4n	.6	4.0	9.4	15.8	20.8	24.8
		Periodic Increment					
20° C.	2n	—	.2	.2	1.1	2.8	2.5
	4n	—	.8	.8	3.0	5.0	5.1
25° C.	2n	.2	1.3	5.3	7.6	9.2	10.0
	4n	.6	2.5	8.8	11.1	12.2	13.3
30° C.	2n	.5	7.8	13.8	10.4	6.4	6.5
	4n	.9	14.0	23.8	14.6	10.2	10.6
35° C.	2n	1.1	11.1	13.0	8.7	6.5	5.4
	4n	2.2	19.1	25.6	13.8	10.2	12.4
40° C.	2n	.6	2.3	5.9	5.7	5.2	3.1
	4n	.6	3.2	5.3	6.4	4.2	4.1

TABLE 2  
 RYE (*Secale cereale*). TOTAL PERIODIC GROWTH AND PERIODIC INCREMENT  
 IN MILLIMETERS PER 12-HOUR PERIOD

		Total Periodic Growth					
		1	2	3	4	5	6
15° C.	2n	—	—	—	2.4	5.3	7.9
	4n	—	—	—	1.2	4.3	7.1
20° C.	2n	—	.9	5.0	9.8	14.1	19.7
	4n	—	.5	3.7	8.4	12.2	17.3
25° C.	2n	—	2.8	8.8	15.8	24.1	34.9
	4n	—	2.1	7.6	14.1	21.7	33.8
30° C.	2n	.7	4.7	11.7	19.5	25.3	31.5
	4n	.4	2.2	6.9	13.7	20.9	31.4
35° C.	2n	—	4.3	10.4	15.4	18.1	22.7
	4n	—	.9	4.0	7.2	11.7	17.0
		Periodic Increment					
15° C.	2n	—	—	—	2.2	3.1	2.6
	4n	—	—	—	1.2	3.1	2.9
20° C.	2n	—	.9	4.1	4.8	4.3	5.8
	4n	—	.5	3.2	4.6	3.9	5.1
25° C.	2n	—	2.8	6.0	6.9	8.3	10.8
	4n	—	2.1	5.6	6.5	7.6	12.1
30° C.	2n	.7	4.0	7.0	7.8	5.8	6.2
	4n	.4	1.8	4.8	6.8	7.2	10.5
35° C.	2n	—	4.2	6.3	5.2	2.7	4.6
	4n	—	.9	2.9	3.2	4.6	5.3

rate of germination of roots. The rye data are characteristic of those found for other grasses where the tetraploids are slower growing than the diploids. The Sudan grass data are the first known to the writer where the tetraploid is faster growing than the diploid, at least for grasses. A possible explanation may be found either in a difference of auxin production or of auxin utilization for the tetraploid compared with the diploid. The change from diploidy to tetraploidy may have a different effect on auxin relations in the Sudan grass than in the rye.

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